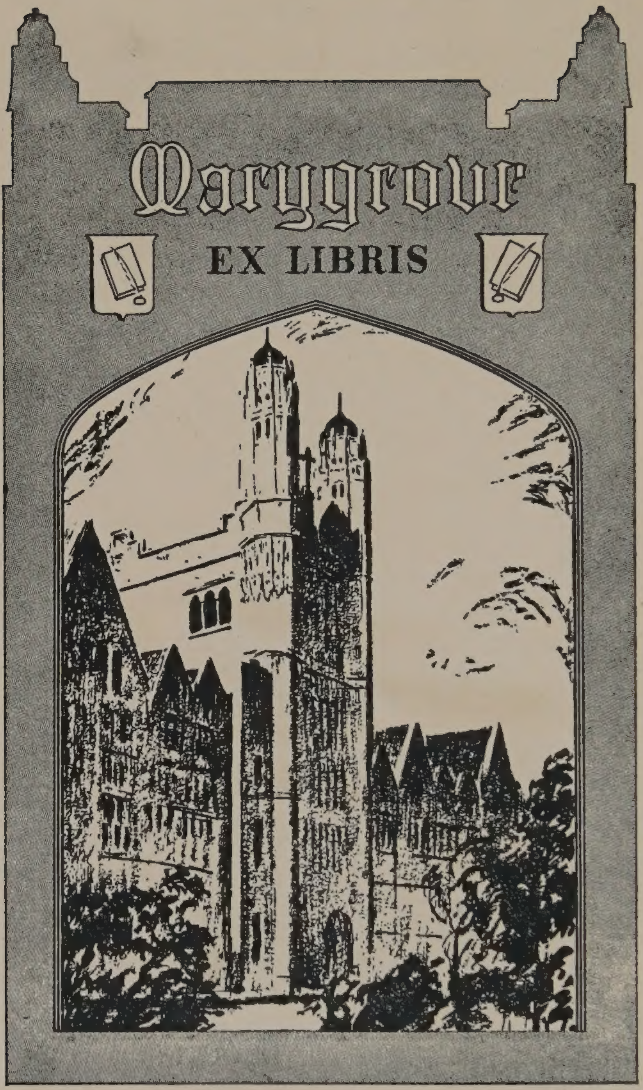

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THE
PHYSIOLOGY OF PLANTS

THE PRINCIPLES OF FOOD PRODUCTION

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PREFACE

THE differences between the author's first book and this one represent the differences due to time, the changes in interest, the changes in perspective, both general and individual. Some of the departures from the usual are by way of suggestion for the future of the science, some for the convenience of the reader.

I have made no attempt to list the bibliography of the many topics touched upon. Believing that all the interested student needs is a start on the bibliography, I have tried to give single references, as recent as possible, containing adequate references to the literature. In cases of dispute two or more references may be found.

Whatever my own opinions about disputed matters may be, I have wished to express them, not as dogma, but as hypothesis or opinion, hoping and desiring always to say what will stimulate rather than satisfy.

I have written no single chapter on Growth, for I cannot conceive of growth as a physiological process apart from the influences to which the self-operating mechanism, the living organism, is subject. The morphological features of growth are treated in the books on the structure of plants. The physiological features of growth are dealt with here under the head of warmth, light, water, and the other factors of the environment, in the chapters on Irritability.

Similarly, leaving to the morphologists the description of the structural or organic features of the subject of Reproduction, I have discussed the factors of the environment which, directly or indirectly, regulate reproduction, either stimulating the plant to fruit or bloom, or producing such conditions in the plant that Reproduction follows.

No man now writes a book without being very conscious of the help given him by his associates. I gladly take this opportunity to thank my colleagues in this University. Also, I wish to acknowledge very gratefully the library facilities which I have enjoyed at Harvard and elsewhere, and the liberality of the Administration of Stanford University in giving me leave of absence when I needed it.

G. J. P.

STANFORD UNIVERSITY, CALIFORNIA,
June, 1925.

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ABBREVIATIONS

(Mainly of Names of Journals)

Abhandl. d. K. Sächs. Ges. d. Wissenschaften	Abhandlungen der Königlichen Sächsischen Gesellschaft der Wissenschaften
Agric. Exp. Sta.	Agricultural Experiment Station
Am. or	
Amer. Journ. Bot.	American Journal of Botany
Amer. Journ. Physiol.	American Journal of Physiology
Amer. Naturalist	American Naturalist
Ann. Chim. et Phys.	Annales de Chimie et de Physique
Ann. de l'Inst. Pasteur	Annales de l'Institut Pasteur
Ann. d. Physik	Annalen der Physik
Ann. Bot.	Annals of Botany
Ann. d. Sci. Nat. Bot.	Annales des Sciences Naturelles, Botanique
Ann. Rep. Smithsonian Inst.	Annual Report of the Smithsonian Institution
Arb. a. d. Bot. Inst. Würzburg	Arbeiten aus dem Botanischen Institut in Würzburg
Beihefte z. Bot. Centralb.	Beihefte zum botanischen Centralblatt
Beiträge z. allgem. Bot.	Beiträge zur allgemeinen Botanik
Beiträge z. Biol. d. Pflanzen	Beiträge zur Biologie der Pflanzen
Ber. d. d. Bot. Ges.	Berichte der deutschen Botanischen Gesellschaft.
Biochem. Bull.	Biochemical Bulletin
Biochem. Journ.	Biochemical Journal
Biochem. Zeitsch.	Biochemische Zeitschrift
Biolog. Centralb.	Biologisches Centralblatt
Bot. Archiv	Botanisches Archiv
Bot. Centralb.	Botanisches Centralblatt
Bot. Gaz. or Gazette	Botanical Gazette
Bot. Jahrb.	Botanische Jahrbücher
Bot. Zeitung	Botanische Zeitung

Bull. Coll. Agric.	Bulletin of the College of Agriculture, Imperial University, Tokyo
Bull. Soc. Bot. de France	Bulletin de la Société Botanique de France
Bull. Torrey Bot. Club	Bulletin of the Torrey Botanical Club
Bull. U. S. Dep't Agric.	Bulletin U. S. Department of Agriculture
Bur. Soils	Bureau of Soils, U. S. Department of Agriculture
Biol. Bull.	Biological Bulletin
Cal. Acad. Sci.	California Academy of Sciences
Carn. or Carnegie Inst.	Carnegie Institution of Washington
Centralb. Bakt. Parasit.	Centralblatt für Bakteriologie und Parasitenkunde
Chem. Ber.	Berichte der deutschen Chemischen Gesellschaft
Comptes rendus	Comptes rendus hebdomodaires de l'Académie des Sciences Naturelles
Contrib. Bot. Lab. Univ. Penn.	Contributions from the Botanical Laboratory of the University of Pennsylvania
Contrib. Hopkins Seaside Lab.	Contributions from the Hopkins Seaside Laboratory
Diss. Univ. Berlin	Inaugural Dissertation, University of Berlin
Dep't Bot. Research, Carnegie Inst.	Department of Botanical Research Carnegie Inst.
Gaz. Chim. Ital.	Gazetta Chimica Italiana
Ges. Abhandl.	Gesammelte Abhandlungen über Pflanzenphysiologie
Inaug. Diss.	Inaugural Dissertation
Jahrb. f. w. Bot.	Jahrbücher für wissenschaftliche Botanik
Jahresb. d. Ver. f. ang. Bot.	Jahresbericht des Vereins für angewandte Botanik
Jenaische Zeitsch. f. Naturwiss.	Jenaische Zeitschrift für die Naturwissenschaft

Journ. Agric. Research	Journal of Agricultural Research
Journ. Bacteriology	Journal of Bacteriology
Journ. Chem. Soc.	Journal of the Chemical Society
Journ. Exp. Zool.	Journal of Experimental Zoölogy
Journ. Gen. Physiol.	Journal of General Physiology
Journ. Indust. and Engin. Chem.	Journal of Industrial and Engineering Chemistry
Journ. Physiol.	Journal of Physiology
Konink. Akad. v. Wetensch.	Koninklijke Akademie van Wetenschappen
Landw. Jahrb.	Landwirtschaftliche Jahrbücher
Landw. Versuchsstat.	Landwirtschaftliche Versuchsstationen
Liebig's Ann.	Liebig's Annalen der Chemie
Lund's Univers. Arsskrift	
Monatsh. d. Preuss. Akad. d. Wiss.	Monatsheft der Preussischen Akademie der Wissenschaften
Naturw. Wochenschr.	Naturwissenschaftliche Wochenschrift
New Phytol.	New Phytologist
Oreg. Agric. Exp. Sta. Bull.	Oregon Agricultural Experiment Station Bulletin
Philos. Trans. Roy. Soc.	Philosophical Transactions of the Royal Society of London
Physiol. Researches	Physiological Researches
Pop. Sci. Monthly	Popular Science Monthly
Proc. Cal. Acad. Sci.	Proceedings California Academy of Sciences
Proc. Roy. Inst.	Proceedings of the Royal Institution
Proc. Roy. Soc.	Proceedings of the Royal Society
Proc. Soc. Amer. Foresters	Proceedings of the Society of American Foresters
Proc. Soc. Exp. Biol. and Medicine	Proceedings of the Society for Experimental Biology and Medicine
Quart. Journ. Microsc. Sci.	Quarterly Journal of Microscopical Science

Recueil d. trav. Bot. Néerland.	Recueil des travaux botaniques Néerlandais
Rend. Acad. d. Lincei	Rendiconti del Academia dei Lincei
Sci. Proc. Roy. Dublin Soc.	Scientific Proceedings of the Royal Dublin Society
Sitzsb. d. Akad. d. Wiss. or *Sitzungsber. Berliner Akad.*	Sitzungsberichte der Akademie der Wissenschaften, Berlin
Sitzungsber. K. Akad. d. Wiss., Math. Naturw. Kl.	Sitzungsberichte der Königlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse
Sitzungsber. d. Heidelberger Akad.	Sitzungsberichte der Heidelberger Akademie der Wissenschaften
Trans. Amer. Inst. Mining Engineers	Transactions of the American Institute of American Engineers
Trans. Chem. Soc.	Transactions of the Chemical Society
Trans. Roy. Soc.	Transactions of the Royal Society
Transl.	Translated by —
Univ. Cal. Publ.	University of California Publications
Univ. Missouri, Coll. of Agric., &c.	University of Missouri, College of Agriculture, Agricultural Experiment Station Bulletin
U. S. Dep't Agric.	United States Department of Agriculture
Unters. a. d. Bot. Inst. Tübingen	Untersuchungen aus dem Botanischen Institut zu Tübingen
Zeitschr. f. Bot.	Zeitschrift für Botanik
Zeitschr. f. Elektrochem.	Zeitschrift für Elektrochemie

THE
PHYSIOLOGY OF PLANTS

I

INTRODUCTION

Plants and animals live in a world consisting of matter and energy. They are themselves composed of matter, of various sorts, and they store and liberate energy, of various forms. Many of the materials of which they are composed, and all of the energy involved in their existence, are found also outside of the bodies of living plants and animals. Living organisms exist, therefore, in a world consisting of living and lifeless things; they use energy which they absorb or liberate; and they must so behave as to be in harmony with these surroundings. They are said to be " adapted " to their environment; but it is difficult to see that they are any more adapted to their environment than is a crystal of common salt, which forms or not, which grows or disappears, according to its environment, and in its own way, peculiar to, and characteristic of the material of which it consists.

In the behavior of plants and animals, therefore, both matter and energy, substance and circumstance are involved, and their behavior is forced by these two sets of factors. One may study the behavior of living organisms from various points of view, calling one's study Animal Behavior, Plant Ecology, Sociology, or what not; but if one study the more intimate processes, those taking place in the living organism or carried on by it, the subject is called Physiology. With this limitation the subject of Physiology is still extensive; for in it are implied knowledge of the anatomy, the chemical composition, the physical condition, of an organism and of its parts; knowledge of the factors constituting the environment; knowledge of the processes going on in the living organism and its parts, and of the connection between these processes and the world outside.

Processes going on in living organisms are commonly spoken of as functions, and physiology is sometimes defined as the study of the vital functions (of living organisms). But though living organisms differ from lifeless things in ways readily recognized, these differences so completely escape definition that one is forced to admit that what we know about plants and animals leads us to recognize in them mechanisms made of matter, and operating with energy, susceptible of chemical and physical examination. Our limited knowledge is the fruit of study facilitated by imperfect tools. Improvement of our tools and correspondingly more penetrating studies lead us deeper and deeper into the intricacies of the living organism and of the conditions and changes prevailing in its most minute parts.

To the physiologist, therefore, the living organisms are the objects of study; but the means are physical and chemical. The physicist and chemist are engaged in studies designed to satisfy their curiosity about the energy and the matter of the world in which they live. The physiologist studies the physicist and chemist or some other living organisms, intent to ascertain the details and to determine the causes of their behavior. The physiologist seems sometimes to be pursuing the same studies as the physicist and chemist; but if he is, his aim is not the same as theirs, for his curiosity is as to conditions and causes in the behavior of the living, and not mainly or exclusively or indifferently in the lifeless. In order to attain his object the physiologist may kill the organism, or he may work with material lifeless from the start; but if he does so, it is with the ultimate aim of learning more about life and living things. We should have known little about anatomy had anatomists limited themselves to exploratory and cytological work on living victims. But just as the anatomist, by his macroscopic and microscopic studies of cadavers, has contributed to knowledge of living plants and animals by revealing their structure in as great detail as is yet possible, so the properly balanced physiologist is engaged in studies which reveal in the greatest detail now possible the conditions, causes, and courses of the processes, functions, and acts of plants and animals. He must keep constantly in mind that living plants and animals appear as plastic as they are complex, in one at least of these respects differing from all lifeless things.

The aim of physiology is the knowledge of living organisms; but in order to understand them, one must also know the conditions under which they live. An exact analytical study of the many factors, living and lifeless, composing the environment of living things is indispensible to an understanding of the things themselves.[1] This involves the study of the earth and its atmosphere, the light and the other forces affecting them, and the other factors more directly operating upon them. One may stop with a knowledge of the earth, and be a geologist, or one may study the earth as the abode of life and so be a biologist. One may study climate and be a meteorologist, or one may observe the weather as a biologist. One may concern oneself with the compounds of carbon and be a chemist, or one may limit oneself to structures consisting largely of carbon but acting as so-called self-operating mechanisms, and be a physiologist. One may study energetics and be a physicist; but the physicist who is engaged with the absorption, storage, and release of energy in living organisms is a physiologist.

One may aim to have adequate knowledge of the composition and structure of plants or of animals, of the physical conditions and processes in them and in contact with them, of the chemical changes resulting in transformation of matter and of energy within them and between them and their environment. These are the goal of the student of the physiology of plants and of animals. Whether with such aims, one study plants or animals is mainly a matter of chance. The vital processes or functions are essentially alike in all living organisms. They are called Nutrition, Respiration, Growth, Movement and Reproduction. They are not peculiar to living organisms, involving any matter or energy found only in them, and, evidently taking place under the same conditions as other processes in nature, they are subject to the same control.

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[1] See L. J. Henderson, *The Fitness of the Environment*, New York, 1913.

In what way, then, should or can we conceive living organisms as different from the lifeless things around them? Are we to conceive a living organism, a living individual, or any of its living parts, as composed of matter or material or substance (chemical compound) itself alive? We are able to see, with the highest power of the microscope, only masses of molecules. The single molecule is still beyond the powers of vision, aided to the utmost. But molecules are conceived to be composed of atoms, all alike or differing from one another, according to whether we are dealing with an element in molecular form as O_2, or a compound, as CO_2. And the researches of electric and other physicists have led to conceptions of electrons as components of atoms. The living individual has living organs. These may remain alive for a time even when separated from the rest of the body. Tissues may be taken from these organs and kept alive. Single cells can be isolated and their life prolonged, with due care.[2] One may divide the cell into still smaller protoplasmic fragments, but sooner or later a point is reached beyond which further division results in immediate death. Yet these fragments are masses of molecules. The molecules, chemical compounds, composing living organisms, are not then alive. Life is resident in or a property of structures or masses of molecules.

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[2] Harrison, R. G., *Journ. Exp. Zool.*, 1907 (p. 140), 1910 (p. 787); Carrel, 1913; Carrel and Burrows, 1912, etc.

Biologists of every sort, therefore, are dealing with masses of matter far coarser than those of the chemist, masses composed of the chemists' units and obeying his laws, but with actions which presumably are the product both of their component compounds and also of their arrangement as structures in space. Protoplasm is the name given to living matter. It exists in nature as larger or smaller masses of viscid, translucent material, alike in its properties but with extremely varied products. These masses of protoplasm are for the most part definitely bounded and are what are called cells, the units of structure and function, though to various organs of the cell are attributed different and specific functions. Protoplasm may therefore be alive, the different portions of a protoplasmic mass may also be alive, but their component chemical compounds are not. Life resides in the structure, it may be conceived to be a property of the structure, called protoplasm.

Subjected to chemical, physical, and microscopic analysis, protoplasm discloses extraordinary uniformity and extraordinarily little else. From examination of the material itself we gather almost no indication of how or why the remarkably varied results of its action are produced. We can but speculate or candidly confess ignorance. But the common results of its activity — the absorptions and excretions, the oxidations and reductions, the growths and divisions, the movements and other responses to stimuli — we can see to be due to the composition and the physical balance of the structure. We should, then, make some study of protoplasm as the physical basis of life.

The Living Substance; Protoplasm

The material in which life is resident and which is commonly said to be itself alive, named protoplasm in 1846 by von Mohl,[3] is finely granular, viscid, refractive, permeable to water and some substances dissolved in water, impermeable to other water-soluble compounds, and many others. While capable of absorbing considerable quantities of water it is insoluble in it. In fact it is insoluble in anything except as it undergoes chemical change. It fixes certain substances which enter it, and is thus said to be adsorptive. And it bears definite relations to heat, two of its physically as distinct from physiologically critical temperatures being the same as those of water, namely the freezing and boiling points. Thus at the freezing and boiling points of water it ceases to be active and will die if either temperature is long maintained. At summer heat, 36° C., it is most active, and hence this is the temperature at which many incubations are best carried on. At 50° C. its activity may be suspended, to be renewed if the temperature falls; but exposure to 60° C. produces permanent inaction in most cases, and is therefore used, in the process called Pasteurization,[4] to destroy organisms which are in the active, vegetative condition.

Protoplasm is sensitive to heat directly in proportion to its activity, but the protoplasm of certain organisms departs from this general scheme of critical temperatures. Thus seeds, spores, or other "resting" stages of fungi, bacteria, flowering plants, algæ, animals, etc., are capable of surviving extremely low temperatures[5] apparently uninjured, whereas freezing would be promptly fatal to most of these same forms were they actively vegetating at the time of exposure. Low temperatures affect epidemics, for example, mainly through killing the active germs of disease; but complete sterilization by cold is generally unattainable by reason of the resistance of the resting forms.[6] On the other hand there are many organisms whose habitat is such that they rarely if ever are exposed to temperatures much above the freezing point of water, and at these temperatures they thrive. Such organisms are the small forms living in cold seas and streams and in cold soils.[7] It will be shown later (page 193) that the maintenance of a body temperature more or less independent of the environment makes it possible for capable organisms to live under otherwise fatal conditions. Thus trout may thrive in extremely cold water, and while their bodies may feel cold to the hand of the angler who takes them, yet their body-temperatures are above those of the water.

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[3] Mohl, H., von, Ueber die Saftbewegung im Innern der Zelle. *Bot. Zeitung,* 1846.

[4] Jordan, E. O., *General Bacteriology.* Philadelphia and London, 1919 or later.

On the other hand, the relation of organisms to high temperatures is much more definite. Presumably the reasons are these: chemical change may be delayed or even stopped by low temperatures, but except as these may affect the *reversible* change from the gaseous to the liquid, and from the liquid to the solid, state of some of the components or contents of protoplasm, they are less injurious than high temperatures. The latter may accomplish *irreversible* changes in the protoplasm, resulting in *coagulation,* which appears to make protoplasmic activities impossible. While many organisms, plants as well as animals, by liberating and retaining heat in their own tissues, maintain temperatures at which their protoplasm can be active in spite of prevailing external cold, no organisms are capable of so cooling their bodies that they can withstand more than very moderate heats. The vegetation of hot springs, geysers and steam vents is scanty[8] in comparison with that of cold waters. Boiling, steaming, baking, and superheating are useful not only for bringing about the chemical and physical changes of cooking; but they are employed in sterilizing the greatest variety of materials.

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[5] Thistleton-Dyer, W. T., On the Influence of the Temperature of Liquid Hydrogen on the Germinative Power of Seeds. *Annals of Botany,* 13, 1899.

[6] Migula, W., *System der Bakterien.* Jena, 1897.

[7] Fischer, A., *Structure and Functions of Bacteria.* English translation by Jones, A. C., Oxford, 1900.

From the foregoing, it is obvious that protoplasm, while resembling water, differs from it both in appearance — it is granular and more highly refractive — and in its relations to temperature. Its granular character may well be attributed to inclusions, the products and by-products of protoplasmic activity. On the other hand, water is an indispensible constituent of protoplasm, the activity of protoplasm varying with the quantity of water available. Drying has been practiced by man for ages as a preventive of decay in wood, textiles, hides, foods, etc. In nature it prevents germination and regulates growth. The proportions of water in various plants and plant organs may be indicated by the following table:

Apples	63.3%	Wood	8–20%
Oranges	63.4	Wheat	10.5
Prunes (dried)	75.6	Ramalina (a lichen)	13.9
Figs "	79.1	Watermelon (whole)	37.5
Tomatoes	94.3	" (edible part)	92.4
Asparagus	94.0		

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[8] Setchell, W. A., The Upper Temperature Limits of Life, *Science*, 17, p. 934, 1903. Davis, B. M., Vegetation of the Hot Springs of Yellowstone Park, *Science*, 1897. Oltmanns, F., Morphologie und Biologie der Algen. 2te Aufl., 3, 364; *Jena*, 1923, and the literature there cited.

The foregoing figures are taken from Leach, A. E., and Winton, A. L., *Food Inspection and Analysis*, 4th Ed., New York, 1920; Wiesner, J., *Die Rohstoffe des Pflanzenreiches*, 3te Aufl., 2, 359, 1918; and Peirce, G. J., Nature of the Association of Alga and Fungus in Lichens, *Proc. Cal. Acad. Sci.*, 3rd Series, Botany, 1, 1899.

Water as a Constituent of Protoplasm

The part played by water in protoplasm may be made clearer by some consideration of its properties. For information about water, a substance occurring everywhere on the earth, we are indebted to the researches of physical chemists; for people in general give little or no thought to it, providing, if at all, only for a sufficient supply in satisfactory purity. The relations of water to heat, light, and other compounds than itself, and its probable structure, have very distinct bearings upon those conditions and changes in living organisms with which we are concerned.[9]

The relations of water to heat, beyond the facts of its solidification and conversion into vapor at certain temperatures, are generally ignored. It is recognized as a poor conductor of heat; but in addition, it has a higher capacity for absorbing heat than any other liquid except ammonia, or any solid, and is therefore taken as the standard of comparison in studies of specific heat. The average amount of heat absorbed by a gram of water the temperature of which rises from 0° to 1° C. is called a mean calorie, which is taken as the unit of heat. The importance of this high specific heat to the protoplasm, and to the whole individual, is obvious; for if it were otherwise — to mention only one thing — the oxidations occurring in the cells of the bodies of plants and animals release quantities of heat sufficient to affect any other chemical reaction as well as the material itself of the organism.

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[9] For fuller discussion of these see Henderson, L. J., *The Fitness of the Environment*, pp. 72–132, 1913, and Bayliss, W. M., *Principles of General Physiology*, 4th ed., pp. 226–245, 1924.

The effectiveness of water in the organism as the stabilizer of temperature is enhanced by its great latent heats of solidification and vaporization. Water freezes at a definite temperature, but as it evaporates throughout a considerable range of temperatures, at rates increasing with the temperature, it accordingly absorbs heat throughout this range, at rates rising with the temperatures. If the temperature of an organism be the same as that of its environment, it can give off heat, if at all, only by evaporation. The regions of highest temperature on the earth's surface are regions of highest evaporation owing to the dryness of the air. Hence the cooling effect of water evaporation from plants and animals exposed to full sunshine, may be of the utmost importance to them.[10]

The translucency of water is very marked, but as it is not equally translucent to all forms of radiant energy, its effects upon the environment (see pages 313–334) as well as upon the organism itself are not uniform. Water absorbs heat rays much more than it does light rays; but of the light rays there is such unequal absorption that, for example, the sky looks bluer or paler in different regions or at different seasons according to the dryness or dampness of the air. But in such thin layers as water exists in the parts of living organisms exposed to light and to other forms of radiant energy, it is practically transparent.

The solvent power of water is not only greater than that of any other liquid, but both solvent and solute undergo less chemical change, or less irreversible change at least, during this relation than in any others now known. The dissolved substance and the water are both recoverable as such, and completely, if desired. On the other hand, it is well known that many substances, and to a certain extent the water itself, undergo dissociation in dilute aqueous solution, behaving, as ions, with a freedom and in ways not possible for their compounds. Thus water not only makes possible many chemical reactions which would not take place among its dissolved substances if they were in contact in the dry state; and it has been suggested that, in addition, water may act as a catalyzer.[11]

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[10] See MacDougal, D. T., A New High-temperature Record for Growth. *Ann. Report, Director Dept. Bot. Research,* Carnegie Inst. Washington, 47, 1921.

The mechanical and other effects of water as a constituent of protoplasm, as indicated by turgescence and osmotic pressure will be considered later (pages 333–348); but it must be recognized here that in these ways, as in the others above described, the rôle of water in the organism is fundamental.

Other Constituents of Protoplasm

Associated with water as the constituents of protoplasm are many substances, even the kinds of which are still only imperfectly known. The actual composition of very few of these has been ascertained. They are known, therefore, as systems composing the mass or material called protoplasm, the microscopic structure of which has long been the subject of speculation and dispute.[12] A clearer apprehension that protoplasm is probably not a simple structure, such as Bütschli's microscopic froth,[13] or an abstraction as Weismann's[14] hypothesis implies, but rather a system or number of systems not of masses merely, but of molecules or even more finely divided matter as well, has led to the general conception that it is a complex colloidal structure, with all that this implies of stability, plasticity, and complexity in physical and chemical relations, and hence in physiological activities.

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[11] Bayliss, *l. c.*, 238–9.

[12] Harper, R. A., The Structure of Protoplasm. *Amer. Journ. Bot.*, 6, 1919.

[13] Bütschli, O., *Investigations on Microscopic Foams.* Transl. by A. Minchin. 1894.

[14] Weismann, A., *The Germ Plasm; A Theory of Heredity.* Transl. by W. N. Parker, 1893.

Thomas Graham in 1861[15] proposed that substances be divided according to their habits of crystallizing or not crystallizing and of filtering or diffusing or not filtering or diffusing through membranes of certain sorts, into what he called crystalloids and colloids. Since he laid the foundations for a very important and interesting new branch of physical and physiological research, known as Colloid Chemistry, investigation has shown that crystalloids may be found in the colloidal condition, and that at least some colloids may be induced by suitable conditions to crystallize. It is therefore more accurate to speak of a colloidal condition or state than of a colloid; but there are certain substances, for example gelatine, which are commonly spoken of as colloids, because we do not ordinarily meet them in any other state. The condition in which most of the ingredients of protoplasm exist in it is the colloidal.

Just as protoplasm is described as viscid, partaking of the qualities of both solids and liquids, so the colloidal state is intermediate between that of solids and of dissolved substances. In the solid state the molecules of a given substance are distributed in space occupied only by the ether. In a state of solution the molecules of the same substance are distributed in space occupied also by the molecules of the dissolving substance. In dilute solution the dissociation of molecules into atoms, ions, and electrons may also take place. But in the colloidal condition groups of molecules, small enough often to behave in most ways like molecules, are so distributed in space as to be in direct contact with the medium in or with which they are suspended. The consistency of any given colloidal system, as of any solution, will depend upon the properties and the proportions of the substances composing it. Thus one may have a jelly consisting of gelatine and water in such proportions that it will stand up, be stiff and elastic, or will quiver or even flow at ordinary temperatures. The temperature, as well as acids, alkalis, salts and organic compounds added to the water, will affect the behavior of the mass of jelly or of any other colloidal system.

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[15] Graham, T., *Liquid Diffusion Applied to Analysis. Philos. Trans. Roy. Soc.*, London, 1861.

We are now prepared to state and to realize that protoplasm is a colloidal mass in which water and a great variety of other substances exist together; the water being the solvent of many of these substances, the medium of colloidal suspension and emulsion of others, thus being external to some and enclosed in others, and therefore held with a firmness which may be overcome only with the application of great force. The various colloidal systems forming the colloidal mass called protoplasm may have only water in common; for they may consist of water and gelatinous substances, *sols* or *gels*, the water being external to and suspending the sol or the gel and therefore escaping with ease, or enclosed within the gel and removable only on the application of many atmospheres of pressure. Or they may consist of water and proteins, complex compounds with large molecules, which are condensation products of amino-acids, behaving like acids toward strong bases and like bases toward strong acids, since they contain both carboxyl and amino groups, giving them these respective properties. Or they may consist of water and of other substances.[16]

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[16] See MacDougal, D. T., and Spoehr, H. A., Components and Colloidal Behavior of Plant Protoplasm, in *Annual Report of the Director of the Department of Botanical Research,* Carnegie Institution of Washington, Year Book, 1920, and elsewhere.

Thus we have, in its static condition, an enormously complex mechanical, physical-chemical, physiological system; but since it does not exist in a perfectly static condition, the complexity of the system is added to directly in proportion to the activity of protoplasm, and its activity is entirely dependent upon the relative proportions of the actions and reactions of the members, inclusions, and products of its component colloidal systems.[17]

Passing from consideration of these physical-chemical properties and relations, further complexity is found in the fact that these colloidal systems, divided into physiological and structural units called cells, form organs in and for themselves. Thus a plant cell ordinarily consists of protoplasm in which a nucleus, chromatophores and one or more vacuoles can be distinguished from the rest. These differ in density, structure, composition, and hence necessarily in behavior. They perform different functions, accordingly. They are themselves colloidal systems separated from each other by membranes permitting dialysis, and when their operations correspond the cell and the organism ordinarily thrive.

As we shall presently see, the chromatophores, which are of different sorts as indicated by their color, are mainly concerned with nutrition, absorbing energy for food manufacture (page 56) or storing the manufactured food (page 174). In parts exposed to the light, these organs, far more than the rest of the cell plasm, enclose liquid pigments which absorb rays of certain wave-lengths, the energy of which is used in combining CO_2 and H_2O into sugar (page 66). In parts to which light cannot penetrate, the colorless chromatophores may fix the sugar which comes to them, precipitating it as starch, or changing it to other compounds more conveniently stored (page 80). The so-called chromoplastids, orange or other colored chromatophores which are found especially in ripe fruits, are, like the chromatophores in the leaves of certain species in autumn, the persistent cell organs from which some of the formerly contained coloring matter has gone. Thus in oranges and other yellow fruits, the green chromatophores in the skin of the young and ripening fruits become yellow as the fruits ripen.

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[17] Further details and the literature cited may be found in Bayliss, W. M., *The Principles of General Physiology*, 4th ed., l. c., 74–110, 1924.

The vacuole or vacuoles of the cell, volumes of dilute solution into which the cell-sap is accumulated in larger proportion though permeating the rest of the cell, is also often a receptacle of pigments as well as of many other substances simple or complex. The vacuole-walls are sometimes called tonoplasts, but this name, implying that the vacuoles are chiefly responsible for the turgescence of cells, is misleading, since turgescence depends upon the amount and composition of the cell-sap which permeates all of the protoplasm of the cell. We shall have to study this relation in connection with the absorption of water and salts.

The nucleus is often spoken of as the most important organ of the cell. This statement is suggestive rather than exact; for just as there are cells lacking chromatophores and vacuoles, except as they may possibly exist in very rudimentary form, so there are cells and even organisms in which the nucleus also is extremely rudimentary.[18] The only part of a cell invariably and necessarily present is the cytoplasm, that part of the protoplasm said to be undifferentiated, the part in which the organs — nucleus, chromatophores, and vacuole — are enclosed. Haberlandt[19] and others have claimed that the position of the nucleus is the center of cell activity; and many authors attribute to the nucleus the major if not the entire control of heredity. To Haberlandt's general rule there are many exceptions, and in criticism of the latter claim it may be pointed out that though the legs carry the horse, still the whole horse and not any one part carries or draws his load. The very striking appearances revealed by microscopic examination of nuclei, at times of division of both vegetative and reproductive cells in animals and plants, have probably, and naturally, led to exaggerated or distorted views as to the rôle of the nucleus in the economy of the cell and of the organism. Recent experiments indeed suggest that the nucleus, its chromosomes, even specific chromosomes,[20] are the carriers of parental characters to the young. It may well be intimated that while this is probably true, this is not the exact truth, for chromosomes are, after all, coarse objects made up of masses of molecules of different, probably widely different, chemical composition, the qualities of which *inhere* in these molecules, *carried* into them by the atoms, ions, electrons, of which they are built. We must ultimately seek in the chemical constitution of the living protoplasm and its organs, rather than in its coarser or finer structures, for the vehicles and the agent of the characters of the organism. To this we shall return later.

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[18] Olive, E. W., Mitotic Division of the Nuclei of the Cyanophyceæ, *Beihefte z. Bot. Centralb.*, 13, Abth. 1, 1904.

[19] Haberlandt, G., *Physiological Plant Anatomy.* Transl. by M. Drummond, London, 1914.

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[20] Morgan, T. H., *The Physical Basis of Heredity*. Philadelphia, 1919. *The Mechanism of Mendelian Heredity*. New York, 1915. Castle, W. E., *Genetics and Eugenics*, 3rd ed., Cambridge, 1924.

II

NUTRITION: ABSORPTION

Many chemical and physical operations go on in the living organism which are identical with those outside. If one were challenged to name the processes, or even a single process, going on only in the living organism, or which would not go on outside the body if the conditions of temperature, pressure, etc., were the same, one would be forced to admit that none is known. Yet anyone is perfectly aware that the sum of the chemical and physical constitution and reactions in certain instances is a living and active organism, and in others a lifeless object. Certain chains of processes constitute what are called vital functions, while certain other chains of processes constitute merely the formation or crystallization of some lifeless material. It seems, at this time, impossible to draw any line sharply separating vital from other processes. It may be possible in the future. It seems better now to acknowledge that they are strikingly alike and to learn as much as possible from comparison of vital functions and lifeless processes.[1]

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[1] In a recent address, Osterhout essays to determine quantitatively the "vitality" of *Laminaria* by ascertaining its electrical resistance. While the electrical resistance of this seaweed may vary with its "vitality," it must obviously be conceived to be a symptom, accompaniment, or product of "vitality" and not its "vitality" itself. Although it may be shown that the electrical resistance follows the laws of chemical dynamics, it is not by any means an inescapable conclusion that the "fundamental life processes" . . . "obey the laws of chemical dynamics." One may well believe so; but it is as necessary to preserve an open mind as it is praiseworthy to seize upon any available means of quantitative study of vital phenomena, their conditions and results. See *Science*, pp. 352–6, 53, 1921.

The so-called vital functions or processes are Nutrition, Respiration, Growth, Movement, and Reproduction. They are affected by prevailing conditions because of the Irritability or Sensitiveness of the organism. These functions are chains of processes, the final results of which are the feeding, energizing, growth, movement, or reproduction of the organism; but no single process or reaction in any chain can be said to constitute the vital function. Thus the process of Nutrition, whether of plants or of animals, consists in a long chain or series of actions, chemical and physical, which result in supplying the living organism with organic and other compounds in forms suitable for incorporation into the protoplasm or for supplying it with needed energy. This chain consists of processes which may be classified as follows:

1. Absorption of raw and other materials.
2. Manufacture of raw materials into foods.
3. Digestion, "assimilation," distribution, and storage of foods.
4. Incorporation of foods into the living protoplasm or other parts of the organism.

It is obvious that though some of these processes appear to go on in sac-like or other organs in the larger animals, they must be and are intra-cellular, for they are all carried on as completely by unicellular plants and animals as by multicellular and highly differentiated ones.

The living organism is nourished by foods which are manufactured from raw materials. These latter are simple compounds soluble in water but in themselves innutritious. The foods into which they are made are complex compounds, digestible, if not directly soluble in water, and themselves nutritious in that they may furnish material or energy for the protoplasm. The food materials are stable compounds, unchanging under ordinary conditions, and therefore requiring the expenditure of considerable amounts of energy to change them. The foods are readily oxidized or otherwise changed, releasing corresponding amounts of energy in the cells in which they are used. The food materials are of almost universal distribution in nature. The foods do not exist in inorganic nature except as the lifeless products or the remains of living plants or animals. The supply of food materials is coextensive with the mass of the earth and its atmosphere. The supply of food is directly proportional to the activity of those agents manufacturing it.

Therefore, while the supply of raw materials for the manufacture of foods is constant and practically inexhaustible, the kinds and quantities of foods produced vary greatly from time to time, and the supply is always limited. Since the procession of the seasons makes active vegetation alternately possible and impossible, on much of the earth's surface, the supply of food fluctuates accordingly. The familiar succession of seed time and harvest is general; it is not limited to the experience of the farmer, but is a phenomenon of nature, the economic consequences of which are but imperfectly apprehended and which must be so prepared for as to assure survival over periods of non-production. This is accomplished in nature by two means — the storage of food at times of rapid manufacture, and the lessened consumption during times of no manufacture. To the morphologist the seeds, spores, tubers, roots and other organs (medullary rays, etc.) employed by plants as storehouses of food are familiar. To the physiologist the lessened respiration, etc., of these parts, or of the plants of which they are parts, are also familiar. But as man has no "resting period," the problem of his food supply is correspondingly different and difficult, one with which the botanist and plant physiologist have too long mistakenly felt themselves not concerned, but to the solution of which their studies should make valuable contributions.

I

Absorption

Organisms and their component cells are seen from the foregoing discussion to be bags or sacs of water, the wall of the bag or sac being the living protoplasm and its products, such as cellulose, etc., the water being the dilute solution containing many substances, which permeates the protoplasm and may be accumulated in special parts called vacuoles. Foods and food materials are said to be absorbed by the organism, by the cell, but since such absorption is into closed sacs, it must take place through the walls of the sacs. Hence the materials so absorbed must pass through the walls of the sacs and must pass into and through the protoplasm in a state of extremely fine division.

The state of finest division of chemical compounds is that of gas or vapor, but as the majority of the food materials and all the foods are solid or at least liquid at the temperatures with which living things are concerned, organisms must supply themselves with these materials otherwise finely divided. This condition is found in dilute solutions. The usual solvent for foods and food materials is water, some of the physical and chemical properties of which we have already enumerated (pages 11–13). It is necessary, therefore, to study solutions in order to gain an idea, at best only approximate, of the means by which animals and plants actually take food or food materials into their component cells, to be utilized or elaborated into usable compounds. We must first examine the condition of the substance or substances dissolved in the water in which food or food materials occur.

Dilute Solutions. Solutions with which plants and animals are ordinarily concerned are dilute,[2] that is the number of molecules of the dissolved substance (solute) is very small in comparison with the number of molecules of the solvent. Hence whether or not there is any chemical interaction between the solvent (water) and the solute is a matter of little importance, so far as the physical or mechanical condition of the solution is concerned. On the other hand, it may very greatly affect the possibility of chemical change and the chemical reactions which may take place in the solution; for, in sufficiently dilute solution, the solute may exist not only as a compound but also, or perhaps rather, as the component atoms dissociated.

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[2] Findlay, A., *Physical Chemistry for Students of Medicine.* London and New York, 1924.

Furthermore, it is claimed by some authors that between the solvent, water, and the solute there may be such a combination that the result constitutes a hydration in definite proportions. Just as crystalline copper sulphate consists of molecules of water in addition to each molecule of copper sulphate, so it is conceived that in a dilute solution some of the molecules of the solvent unite with molecules of the solute, thus forming groups which behave, physically and chemically, somewhat differently from the anhydrous solute. In answer to this question the physiologist must pursue the methods of physical chemistry or depend upon the physical chemist. The effect of such hydration upon absorption, adsorption, and other "vital" processes has not at present been shown to be very great; but we should, as far as possible, visualize the conditions within and without the living cell and be thereby the better prepared to apply to physiology the fruits of development in physics and chemistry.

There are certain quite elementary considerations which may, without impropriety, be mentioned at this point. Among these is the relative freedom of molecular as well as molar movement in the same substance according to its state of solid, liquid, or vapor. Thus while a cube of ice one centimeter square on each face will retain its shape for a time even at ordinary temperatures, yet the water formed by its melting will settle and spread over its support as it becomes liquid, finally diffusing as vapor through an indefinite volume of air. The stability of the cube of ice and the flow of water are molar phenomena, whereas evaporation from ice and from water are molecular movements. But molecular movement takes place in solids, liquids, and gases, the rate and the amplitude varying with the state, as well as with the temperature and pressure. That molecular movements occur in solids is illustrated by the slow crystallization which takes place in steel rails, the structure of which is quite amorphous as the rails leave the mill. But the relatively low rate and slight amplitude of molecular movement in the solid state is obvious in both ice and steel. As previously pointed out, however, water evaporates — *i.e.*, its molecules leave the mass — at all temperatures, thus revealing an amount of energy of motion quite remarkable.

The shape and consistency of any given mass, solid, liquid, or gaseous, depend, among other things, upon the rate and extent of the movements of the component molecules. The rate and amplitude or extent of molecular movement express the energy of motion of the molecules, and will vary with the temperature and pressure. Thus the shape, size, permanence, and even the existence, of a piece of ice depend upon the rate of those movements which result in successive molecules leaving the mass; and this rate will vary with the temperature and pressure. Thus the ice will last long at low temperatures, though even at temperatures below the freezing point it will not last forever because evaporation continues even then. But as ice, water, and steam evaporate more rapidly into dry air than into moist, we should consider the basis of this phenomenon also.

Air, a mixture of gases, each of which may dissolve other gases, will, in consequence, act as the solvent of a considerable variety of substances. Water is one of these substances; it will dissolve in air, but only up to a certain point. Furthermore, the solvent power of air will vary with its temperature, the higher the temperature, other things being equal, the greater its capacity to dissolve or absorb water. Saturation with water at any given temperature is taken as 100%. The amount of moisture in the air at any given temperature is stated therefore in percentages of this amount, seventy-five per cent for example indicating three quarters saturation; and this indicates the humidity of the air at that temperature. It is obvious that air, like other solvents, will dissolve water fast or slowly according to its humidity at the prevailing temperature, slowly, if it is nearly saturated, swiftly, if its humidity is low.[3] Plants and animals lose water by evaporation and exhalation rapidly if the humidity is low and the temperature high, slowly if the humidity is high and the temperature low. Thirst, whether of animals or of plants, and the absorption of water to satisfy it, are profoundly influenced therefore by the temperature and humidity of the air.

Furthermore, atmospheric humidity tends to regulate atmospheric temperatures; and high atmospheric temperatures are the more endurable the lower the humidity, *provided* there is an adequate and suitable supply of water. As we shall see later (pages 333–348), other structures, as well as those concerned with absorption, are also directly concerned with air dryness or moistness and develop accordingly.

Pressure and partial pressure. So far as we are concerned, and because we are within it, the atmosphere is practically unconfined. But if we imagine suspended in the air a toy balloon filled with the usual ingredients of the air, and another of the same size filled to the same pressure but with a mixture of gases one of which can go through the wall of the balloon, we shall see the one remaining plump and full while the other undergoes a more or less prompt collapse. The molecules of the different gases beat against the walls of the balloons. The molecules of the one gas only escape, and to this extent — the partial pressure of this gas — the balloon collapses. Let us now imagine a toy balloon with wall permeable to one of the ingredients of the air but not to all, and filled with air of the same temperature and pressure as the air outside. There will be no evident change except from leakage due to defective manufacture, for the movements of the one gas through the wall outward and inward will be equal. But if the pressure within the balloon be higher than without, only one of the gases being able to pass through the wall, that gas will flow through the wall out into the unconfined air and at a rate proportional to the difference in its partial pressure within and without the balloon. The molecules of gas will flow down its gradient at a speed proportional to the steepness of the gradient. As the difference in pressure, the steepness of the gradient, between the interior and exterior of the balloon decreases, the rate of movement will correspondingly decrease until, with equal pressures, the outward movement will not exceed the inward, and an equilibrium will be established. This result illustrates what Bancroft[4] calls a "new law of nature," the principle of Le Chatelier, that "a system tends to change so as to minimize an external disturbance." This is also sometimes called the law or the principle of least action.

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[3] Another way of stating the same thing, and a way which may be preferable from the point of view of the physical chemist, though not from that of the United States Weather Bureau, is that, since water molecules are constantly leaving and entering a mass of water or any wet object, the rate of evaporation represents the difference between the rate at which molecules are leaving the mass and the rate at which they are condensing upon and entering or becoming a part of it.

If one regard the atmosphere, as one may, as a solution, rather than merely as a mixture of gases, — though what the actual physical difference would be, cannot be stated — one may perhaps the more readily compare and the more easily understand the behavior of substances dissolved in water. For the air may be thought of as a solution of oxygen, and a number of other more or less active gases, in nitrogen, which is quite inert. Each of these gases, while contributing its share to the total pressure of the atmosphere, consists of molecules moving at their own characteristic speed, exerting their own pressures, having their own characteristic affinities, and combining in characteristic ways with such other molecules as they may encounter. Such is also the condition of substances in dilute solution in water.

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[4] Bancroft, W. D., A Universal Law. *Science*, 1911.

Membranes. We are concerned, among other things, with what appears to us to be a single unconfined and enormous volume of air, and on the other hand with an enormous number of confined and often very minute volumes of water. These volumes of water, enclosed by layers of cellulose produced by and surrounding the protoplasm, are contained in sac-like masses of protoplasm (see page 22). Because of its optical properties we are able to recognize the cellulose wall surrounding a plant cell as a definite membrane. We may also think of the protoplasm itself as constituting a second membrane enclosing water in a vacuole. But in many cells, and presumably at times in all cells, there is no visible vacuole, the water permeating the protoplasm and the cellulose wall. If this be the case, then the water throughout the plant and animal body may be considered to be in fact continuous, being divided only in appearance by walls or membranes or septa of cellulose, protoplasm, etc.; and the individual land plant or land animal constitutes a larger or smaller confined volume of water or aqueous solution. But even this conception fails us in the case of plants, for their root-hairs or other water-absorbing organs connect them with the soil or other water; and water in aquatic plants and animals is obviously continuous with the water in which they live. But as the water in a cell may hold in solution some pigment which does not pass out of the cell, so long as the cell is alive — for example the red and brown seaweeds and the roots of red beets — it is obvious that, however permeated by water the protoplasm and the cellulose wall may be, at least the protoplasm does not seem to be permeable to all substances. The protoplasm itself, therefore, constitutes a partially permeable, a so-called semi-permeable or selectively permeable membrane. We must, however, go further in our analysis; for we realize that, while we are able to distinguish between the protoplasm and its enclosed water only when the water is accumulated in a vacuole, we can almost always distinguish the nucleus and often also chromatophores; and in the protoplasm itself, perhaps a clear apparently homogeneous layer (hyaloplasm) and one which is granular. At times other structures become distinguishable. Now while these organs or parts are distinguishable by observation alone or by observation aided by stains or other means, they are so distinguishable not because they are soaked with parts of a continuous mass of water, but because their constituent materials cohere instead of merging with adjacent materials. We must therefore conceive of them as so built as to constitute definite structures. These structures, unlike the chemists's models of molecules and atoms,[5] must be conceived to be bounded, on their faces where they are in contact with other similarly substantial structures, by a material layer, a membrane, and not merely by a geometrical position. Vacuoles, nucleus, chromatophores, and the protoplasm itself where it is in contact with a cell wall, must be supposed to be enclosed within membranes, permeable to water, impermeable to certain other substances though these may be soluble in water.

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[5] See Langmuir, I., The Structure of the Hydrogen Molecule and the Hydrogen Ion. *Science*, 52, 1920.

Many divide the plant membranes with which the student of absorption is occupied into two classes, those formed of carbohydrates mainly, and those composed mainly of proteins, respectively, (*a*) the cellulose and other cell walls, and (*b*) the cytoplasmic, nuclear, and vacuolar membranes. The cellulose walls may be added to by infiltration or modified in other ways, but nevertheless they possess fairly permanent qualities of which some of the most remarkable are the combination of great mechanical strength with lightness, pliancy, elasticity, and permeability. Contrasted with the slow and generally invisible changes in the cellulose membranes, the cytoplasmic membranes of plant cells, while pliant and elastic, are mechanically weak, and their permeability may be promptly and profoundly changed and reversed. The cellulose membranes are plainly visible; the cytoplasmic membranes are generally not visible and hence their existence, if real, must be inferred from other evidence, such as that of confined pigments (page 28), ultra microscope,[6] dark field illumination,[7] turgidity (page 164), as well as the contributions of cytologists.

These colloidal membranes may be compared with sieves, through the pores of which molecules of suitable size and shape pass freely while others too bulky are held back. We must add this, however, to our conception, for we must think of these sieves as being immersed in water, their pores being filled with water, for it is only dissolved substances which pass through. Carbon dioxide and oxygen do not pass through dry protoplasm and dry cell walls, and as these gases come from air into a living cell, they dissolve in the water permeating its membranes, cellulose and cytoplasmic.

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[6] Zsigmondy, R., and Bachmann, W., Handhabung des Immersions-ultramikroscops. *Kolloid Zeitschrift*, 14, 1914.

[7] Siedentopf, H., Ueber Teilchengrösse in Hydrosolen. *Zeitschrift f. Elektrochemie*, 12, 1906; and Zsigmondy, R., Ueber Sichtbarmachung und Grössenbestimmung untramikroscopischen Teilchen. *Ann. d. Physik*, 10, 1903.

Movements of dissolved substances occur from part to part of the same volume of solvent; they occur from volume to volume only when these volumes are in contact and are therefore virtually continuous. A plant can absorb water only when it is in contact with water, when water molecules touch it and mingle with its water molecules. In order to secure a sufficient supply, therefore, of water and of gaseous and other dissolved food materials, plants must provide sufficiently extensive contacts with the solutions from which material is to be absorbed. In the case of most aquatic plants sufficiently extensive contacts are afforded by the general surface of the body; but *Fucus,* and some of the other larger brown seaweeds living between the tide-marks on the seashore, have their general surfaces so waterproofed to escape undue evaporation while not covered by the tide, that the hairs filling their so-called sterile conceptacles perform the function of connecting the solution within the plant with the sea water. Land plants absorb moisture mainly from the soil. By means of scales, hairs, etc., contact is established between the solution within the plant (its sap), and the solution in the soil (soil water). Mosses and liverworts are the chief land plants making use of scales for water absorption, whereas the larger land plants develop on their roots hairs which, applying themselves to the soil particles (see pages 341–342), establish contacts between the soil water and the sap. These root hairs are said to increase the area of the absorbing organs; but in view of what has been said above, we see that it is not the area of the absorbing organs themselves but rather the area of the contact between the water in the soil and the water in the plant, that is significant. Similarly carbon-dioxide and oxygen molecules, entering the plant through stomata, lenticels, etc., and diffusing through the intercellular spaces, come into contact with the wet walls of the cell which they are to enter and, dissolving in the water of the cell-wall, pass through like other solutes. The intercellular spaces, in leaves and elsewhere, forming continuous passages with the stomata, afford the contacts between the cells abutting upon them and the gases to be absorbed and discharged. (See pages 51–55.)

In many instances the two volumes of solution in direct contact or separated only by a membrane differ only as to the solutes, the solvent being the same, while in other cases the solvents are different and may not mix even when brought into intimate contact. The latter condition prevails, for example, when drops of oil, in which other substances may be dissolved, form part of the contents of a cell. When a substance soluble in both solvents is present in the one or the other of these two immiscible liquids in contact, or separated only by a semipermeable membrane, the solute may pass from the one to the other. Use is made of this to extract water-soluble substances from oily mixtures, the process, if taking place through a membrane, being called dialysis, and the membrane a dialyzing membrane or dialyzer.

Diffusion, Osmosis, Dialysis. While movement of a gas in vapor may be called diffusion, and movements of dissolved substances in a solution may also be called diffusion, diffusion through a membrane has been called osmosis when the solvents on the two sides of a membrane are the same or miscible liquids, and dialysis when the solvents are immiscible. Therefore, the absorption of water and other food materials from the soil by the roots of land plants, and all the absorption by submersed aquatics, may be called diffusion or osmosis, while the absorption of carbon-dioxide and oxygen from the air, in which they are dissolved in nitrogen, which is insoluble in water and will not mix with it, is strictly speaking dialysis. Fundamentally, the three processes are identical, and it is a pity that they should not be called alike, diffusion.

In certain instances there appears to be still further complication in that, between the air, with its carbon-dioxide and oxygen dissolved in nitrogen, and the wet interior of the plant, there is interposed a cuticle or cuticula, forming the outer surface of many epidermal cells, or several or many layers of cork, both of which are quite insoluble in water and impermeable to it. But it appears [8] that carbon-dioxide and oxygen, soluble in nitrogen and in water, are also soluble in the water-proofing materials of these walls. Hence these two gases enter and leave the plant with considerable freedom, by dialysing into these cell walls from the air or from the cells, and from them again into the cells or into the air, respectively, at the same time that very little water is lost through them.

Our exposition has so far been devoted mainly to the mechanisms involved in absorption, and we have considered the physical-chemical properties of dilute solutions, of membranes, of diffusion, osmosis, and dialysis; but we have yet to show the forces by which the mechanisms are operated and absorption actually accomplished. In the first place, as is well known, the word absorption implies a drawing or sucking in. In animals provided with the requisite muscular and other apparatus there is an actual drawing or sucking in of liquid and other food through the mouth into the stomach and intestines. This food, after digestion, is not drawn or sucked into the circulatory system of the blood and the lymphatics but, like the food of all other animals and plants, and the food materials out of which green plants make food, it moves as molecules in solution in water through semi-permeable membranes and by this means presently enters the cells which it nourishes. The forces accomplishing these movements may be two: the energy of motion (kinetic energy) of the molecules themselves of the solute, and also the attraction which the molecules of many substances have for the molecules of other substances.

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[8] Wiesner, J., and Molisch, H., Untersuchungen über die Gasbewegung in der Pflanze. *Sitzungsber. K. Akad. d. Wiss., Math. Naturw. Kl.*, Vienna, 98, 1890.

We have seen that the rate and the amplitude or extent of vibration of the molecules of a given substance vary with the state — solid, liquid, and gaseous — and the temperature, etc., of the material, and are characteristic of it. In solution the molecules move as if they were in the gaseous condition at that temperature. The obstacles in the way of their movement are each other, the molecules of other solutes, and of the solvent, and the bounds of the solution. If these bounds are formed of glass or any other impenetrable material, the molecules recoil as they strike them and move off accordingly, remaining in the original solutions. If the bounds are penetrable, or permeable, the molecules pass through them, and enter another solution or another volume of the same solution. What does the force amount to which accomplishes this movement, both within a solution and from solution to solution? The answer to this physiological question is in the terms of physics, and the means of answering is physical-chemical experimentation.

We may begin this examination by distinguishing, for the moment, between the movement of water and the movement in it of dissolved substances, and by stating that the absorption or entrance of water into a cell will depend upon the difference in the densities of the soil water and the cell sap, whereas the entrance of any solute will depend upon the composition of the cell sap. If, for example, the cell sap be denser than the soil water, *i.e.*, poorer in water, water will enter, will be absorbed, if possible; and if the cell sap be poorer in a potassium, calcium, or other salt dissolved in the soil water, that salt will enter, will be absorbed, if possible. What constitutes possibility, as has been pointed out above (page 30), is contact of the two volumes of liquid and permeability of the intervening membranes, at ordinary temperatures.

Nearly one hundred years ago Dutrochet's[9] study of the pressures involved in the absorption of water was published; but the work was given definiteness and its present form nearly a half century ago by Pfeffer's now classical experiments[10] in which he used Traube's celebrated precipitation membrane of copper ferrocyanide[11] supported in a porous clay cup. The principle involved in the preparation of the apparatus is that of forming across the openings in a porous but strong cup a membrane of great delicacy freely permeable to water but impermeable to certain substances dissolved in water. It is obvious that if such a cup be filled with pure water and submersed in another volume of pure water so that the levels of the two volumes are the same, water molecules will pass with equal freedom through the membrane into and out of the cup. If this be the case, there will be no change in the volume of the liquid inside and outside of the cup, and with the levels the same, the pressures will also be the same. If now a lump of sugar be dropped into the pure water within the porous cup and the level of the water outside raised immediately, if necessary, to the same height by adding pure water to it, the level of the solution in the cup will quickly begin to rise. This rise in level, indicating an increase in volume, is found to be due to an increase in the amount of water inside the cup, an increase which will correspond without being exactly proportional, to the amount of sugar added. If we suppose that no increase in volume in the liquid inside the porous cup is possible, then there will be a corresponding increase in pressure. By applying a mercury manometer to the porous cup, this pressure can be measured. The pressure thus indicated shows some part, at least, if not all, of the force with which water molecules enter cells. Some of these pressures are as follows: Pfeffer found, for example, that at 15° C. and under the conditions above described, a four per cent solution of cane sugar will develop a pressure of 208.2 cm. of mercury. The pressure of the atmosphere at sea level on the equator is 76.0 cm. of mercury. Hence the maximum diffusion pressure which such a solution would develop immersed in sufficient water would be nearly two and three quarters atmospheres, or over forty pounds to the square inch.

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[9] Dutrochet, R. J. H., Nouvelles observations sur l'endosmose et l'exosmose, et sur la cause de ce double phenomène. *Ann. Chim. et Phys.*, 35, 1827.

[10] Pfeffer, W., *Osmotische Untersuchungen.* Leipzig, 1877.

[11] Traube, M., Experimente z. Theorie d. Zellenbildung und Endosmose. *Arch. f. Anat. u. Physiol.*, 1867.

In this case the pressure of water inside and outside the porous cup was supposed to be the same, but dropping a lump of sugar into the cup caused an increase in volume or pressure inside the cup. We must assume that the water molecules which did not freely pass inward and outward struck the membrane with equal force on the two sides, but when a lump of sugar goes into solution in the cup, the walls of the cup are struck not only by water molecules on both sides but on one side by sugar molecules also. Thus there will be an immediate increase in osmotic pressure within the cup, an increase proportional to the number of sugar molecules which dissolved in the water. Hence, roughly,[12] the more concentrated a solution, the greater its osmotic pressure, other things being equal. It should be borne in mind, however, that different substances may exert different osmotic pressures.

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[12] Morse, H. N., The Osmotic Pressure of Aqueous Solutions. *Carn. Inst. Wash. Publ.*, 198, 1914.

Osmotic Pressures of Different Substances[13]

Substance	*Concentration*	*Osmotic pressure in Atmosphere*
Cane sugar	0.1 gr. mol.	2.474
Grape sugar	0.1 " "	2.475
Mannite	0.1 " "	2.468
Lithium chloride . . .	0.1 " "	4.317
Potassium chloride .	0.5 " "	20.6

That sugar molecules, whether in a dry mass or in a solution, can attract water molecules is a matter of ordinary experience. This is a common property of many substances, solid, liquid, and gaseous; but the attraction varies according to the substance as well as its concentration. Thus common salt, calcium chloride, copper sulphate, glycerine, alcohol, air, and many others, attract water, becoming sticky, deliquescing, changing in color, or giving other evidence of water absorption. But equal masses of common salt and calcium chloride exposed side by side will absorb water from the air at characteristically different rates. In solutions of equal concentrations their osmotic pressures will be characteristically different, as proved by experiment.

When we realize that the liquid in the cells of plants and animals is an aqueous solution of many different substances, organic and inorganic, we realize that its attraction for water will correspond. That this attraction is great was shown, though only imperfectly, by de Vries,[14] the defect in de Vries's experiments being due to the incomplete impermeability of the membranes of living cells. Even the copper ferrocyanide membrane of Traube is slowly, though very slowly, permeable to sugars and to other substances commonly occurring in cells. It must, however, be conceded that, for membranes as thin as many cytoplasmic membranes are, their impermeability is very remarkable. Comparisons of membranes as to permeability are of less value, however, than at first appears, because it is often impossible to experiment upon membranes of equal or uniform thickness. The membranes, for example, apparently perfectly impermeable to the pigment of red beets, and to the cane sugar of sugar beets, are of microscopic thinness or less, whereas experiments are conducted with animal bladder, parchment paper, and artificial precipitation membranes. De Vries and his successors[15] have shown that living cells of plants, of kidney, and of muscle, will absorb water and expand, or will lose water and contract, according to the concentration of the solutions in contact with them. Experience shows, for example, that a three per cent solution of potassium nitrate, the osmotic pressure of which is approximately eleven atmospheres, exerts the same pressure as the sap of the majority of the cells of land plants living under the usual conditions. The investigations of Harris[16] and others into the concentrations of the cell-sap of plants living in the "rain forests" of the humid tropics and subtropics, of Fitting,[17] and others who studied desert plants,[18] and of Oliver and Hill,[19] who studied the halophytes of salt marshes, show that the concentrations of cell-sap correspond with the concentration of the waters of the environment. Reflection will at once show that marine plants must have denser cell-sap than those living in fresh water.

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[13] From Morse.

[14] Vries, H. de, Eine Methode zur Analyse der Turgorkraft. *Jahrb. f. w. Bot.*, 14, 1884.

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[15] See for citations, Bayliss, *l. c.*, p. 115 *et seq.*

[16] Harris, J. A., Physical Chemistry in the Service of Phytogeography. *Science*, 46, 1917. *Amer. Journ. Bot.*, 1, 1914; 2, 1915. *Biol. Bulletin*, 32, 1917. Harris, J. A., Gortner, R. A., Hoffmann, N. W., Lawrence, J. V., Valentine, A. T., Osmotic Concentration, Specific Electric Condition, and Chloride Content of the Tissue Fluids of Indicator Plants of Tooele Valley, Utah. *Journ. Agric. Research*, 27, 1924.

[17] Fitting, H., Die Wasserversorgung and die osmotischen Druckverhältnisse der Wüstenpflanzen. *Zeitschr. Bot.*, 3, 1911.

[18] Livingston, B. E., The Relation of the Osmotic Pressure of the Cell-sap in Plants to Arid Habitats. *Plant World*, 14, 1911.

[19] Hill, I. G., Observations on the Osmotic Properties of the Root Hairs of certain Salt Marsh Plants. *New Phytol.*, 7, 1908. Drabble and Lake, similarly in *New Phytol.*, 4, 1905, and *Bio-Chem. Journ.*, 2, 1907.

CELL-SAP CONCENTRATIONS IN ATMOSPHERES

	Woody	*Herbaceous*
Montane rain forest:		
Blue Mts., Jamaica	11.44	8.80
Mesophytic region:		
Long Island, N. Y.	14.40	10.41
Saint Louis, Missouri	14.96	
Desert regions:		
Jamaica coastal deserts	30.05	
Arizona deserts	24.97	15.15
Salt marsh		
Jamaica		38–49
Epiphytes		
Jamaican rain forest		2.8–5.5
Parasites		
Generally more concentrated than hosts		

Many of the lower plants exhibit extraordinary tolerance and powers of adjustment to changing concentrations of the surrounding water. Plants which live submersed in the mouths of fresh water streams emptying into the sea may be subjected twice daily to sea water and to water completely fresh. Species of *Enteromorpha* and *Cladophora* may be mentioned. The plants and animals living in outfall sewers at their entrance into the sea may be exposed to very rapid and repeated fluctuations of the concentration of the solution bathing them. The algæ growing on the bottoms of vessels plying between fresh and salt water ports [20] offer further examples of osmotic readjustments; and the plants and animals of the salt and alkaline lakes of the West, at least one of which is undergoing gradual concentration at the present time,[21] afford striking examples of the capacity of living cells to form saps which are solutions of great concentration and unusual composition. The Great Salt Lake of Utah receives direct additions of fresh water in the form of rain and snow, and from the mountain streams of the region. These change its concentration as a whole but slightly, but produce great local changes, to which its inhabitants, mainly unicellular plants, insects and animals still lower, must conform quickly or perish. The plants of salterns, in which salt is made on a commercial scale, are exposed to solutions of great concentration.[22] The simple experiment of exposing brine plants to a drop of distilled water under the microscope shows at once the permeability of their cell membranes to water; and the prompt change in shape and size shows the concentration of their cell-sap. In fact, studies of the permeabilities and other properties of organisms living under these and other adverse conditions would undoubtedly be very rewarding.

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[20] Osterhout, W. J. V., The Resistance of certain Marine Algæ to Changes in Osmotic Pressure and Temperature. Univ. California Publ., *Botany*, 2, 1906.

It is further to be noted that the concentration of the cell-sap in different parts of the same plant or in the same parts at different times may not be the same. Thus I have repeatedly noticed that while a 3½ per cent KNO_3 solution may have the same density as (be isotonic with) the sap of cells of hairs on the leaves of Hubbard squash on the cool foggy mornings in the Experimental Garden of Stanford University, a four per cent solution is found to be isotonic on the warm sunny afternoons, in the latter part of the rainless dry season. Two things are to be observed in this connection: water will be lost by evaporation less and less rapidly from these cells as their sap concentrates, and they will absorb water from adjacent cells and otherwise more and more forcibly and rapidly whenever absorption is possible.

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[21] MacDougal, D. T., and collaborators, *The Salton Sea: A Study of the Geography, the Geology, the Floristics, and the Ecology of a Desert Basin.* Carnegie Inst. Wash. Publ., 193, 1914.

[22] Peirce, G. J., The Behavior of certain Micro-organisms in Brine. *The Salton Sea,* pp. 49–69, 1914.

Two other factors must be spoken of in considering the absorbing powers of plant and animal cells, namely the *adsorption* of material by the membranes, and the condition of electrolytic dissociation of many substances in dilute solution. The latter produces higher osmotic pressures, other things being equal, than the same substances undissociated.[23] In consequence both the absorbing powers of cells containing dissociated atoms and also the possible chemical changes within the cells are correspondingly increased.

As to *adsorption* phenomena the conservative physiologist may feel that more has been written than is justified by what is at present known. Nevertheless it is a conception based on actual observations which should not be ignored.[24] The soil adsorbs a great variety of substances which otherwise might be very dangerous to plants and animals (*e.g.*, copper salts). It is claimed that the seaweeds which furnish us with iodine and its compounds accumulate their iodine content by adsorption from the excessively dilute solution of iodine in seawater.[25] Whether this guess has any other merit than novelty, as compared with the old idea of the iodine accumulating as a by-product of metabolic processes, it is still too early to say.

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[23] See Arrhenius, S., Faraday lecture, *The Theory of Electrolytic Dissociation.* Trans. Chem. Soc., 105, London, 1914.

[24] See Bancroft, W. D., *Applied Colloid Chemistry.* New York, 1920.

[25] Hatschek, E., *Introduction to the Physics and Chemistry of Colloids,* 3d ed., pp. 15–16. London, 1919.

Summary

We see that absorption, both of food materials and foods, of solids, liquids, and gases, both by organisms and by their component cells, takes place in solution in water through membranes permeable to water but not necessarily to substances soluble and dissolved in it, in consequence of osmotic pressure and molecular attraction, electrolytic dissociation and adsorption increasing the rate at which absorption takes place. Given semi-permeable membranes, containing water, and in contact on one side with the cell sap and on the other with soil water or other solution containing water-soluble solutes, absorption will take place whenever and as long as differences in concentration and in composition exist between the solutions inside and outside the cell. The force with which absorption is accomplished is so considerable as to be measured in atmospheres, and is approximately proportional to the concentration and the osmotic pressures of the solution and solutes concerned.

III

NUTRITION: FOOD MANUFACTURE

Carbon

THE most important chemical reaction in nature is that which converts inorganic food material into food. It is impossible, from the standpoint of living organisms, of man and other animals, as well as plants, to overestimate the value of this combination. It cannot be adequately expressed in any terms whatsoever, whether in figurative language, which states that it is the single barrier between living organisms and death by starvation; or in terms of money, in which the following figures of crop production in the United States of America must be regarded as merely suggesting the whole yield and its value in this country,[1] to say nothing of the rest of the world. The Secretary of Agriculture says: "On the basis of prices that have recently prevailed, the total value of all crops produced in 1919 is $15,873,000,000. The value of live stock on farms in 1919 was $8,830,000,000. The National Forests sold timber to the value of $1,503,367, and grazing permits which brought into the National Treasury $2,556,962." If one add to this the value of pulp, straw, and other products and by-products of farm, field, and forest, in private and public ownership, one will have a sum almost inconceivably large, even in these times of huge figures, but representing, after all, only a small fraction of the total annual production of the most important synthetic process in nature.

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[1] *Year Book U. S. Department of Agriculture*, Washington, 1919, and *Year Book U. S. Department of Agriculture*, Washington, 1923. "Taking the value of the 11 crops — corn, wheat, oats, barley, rye, buckwheat, flaxseed, potatoes, sweet potatoes, hay, and cotton — as of October 1, except in the case of corn (which is taken at the December future prices as recorded for the first 15 days of October), we find that this value was $5,289,000,000 for 1921, $5,711,000,000 for 1922, and $6,947,000,000 for 1923. In neither year does the sum indicated include the total value of farm crops grown."

The great interruption to production and distribution, both local and general, occasioned by the war of 1914–18, has once more called attention to the dependence of man upon the food produced, season by season, by green plants. It has become evident that there is no store of food in nature, as there is of coal or iron, that there is no unfailing source, as there is of water, and that time is as much a factor in food production as the raw materials. Reflection shows that man is willing to jeopardize the permanent security of his food supply for the sake of temporary convenience or cheapness, and that he prefers to honor and reward the manipulator rather than the producer. It behooves us, therefore, as citizens as well as physiologists, to investigate the processes of food manufacture, and, if we can, throw new light on the problem of world-old hunger.

The raw materials, absorbed into cells by means treated in the preceding section, come, in solution in water, from the soil and the air. This statement applies equally to aquatics and land plants, for the salts in solution in salt and fresh waters come from the land, and the oxygen and carbon-dioxide from the air. The raw, or food, materials are simple saturated compounds, soluble in water, and not in themselves nutritious, their constituent elements or ions being rearranged in new combinations, complex, unsaturated, soluble in water at least after "digestion," and themselves nutritious, furnishing material or energy. The distinction here attempted, between food materials and foods, is of little practical value at the present moment because of the common application indiscriminately of the term "plant food" to those inorganic as well as organic materials in or added to the soil in agricultural practice. It is, however, perfectly obvious that, chemically as well as physiologically, food materials and foods are much more unlike than, for example, the raw material cotton or iron and the cloth or utensil made from them.

The food materials are carbon-dioxide (CO_2), oxygen (O_2), water (H_2O), and the mineral salts containing potassium, calcium, magnesium, nitrogen, sulphur, phosphorus, and iron. The usual mineral salts are the nitrates of potassium and calcium, the sulphates of magnesium and to a lesser extent of other alkaline elements, and the phosphates of potassium and iron. Because of their universal distribution, sodium and chlorine, in combination with each other or with other elements, are invariably shown by analysis to be present in plant and animal material. However indispensible they may be to animals,[2] they seem not to be necessary to plants. In the water cultures of many sorts now in use (see pages 123–125) these two elements are not deliberately included; but to exclude them completely, and continuously, is very difficult, as may be seen by reading Pfeffer's account of the experiments carried out in his laboratory and elsewhere with this intent.[3]

The ten elements above enumerated — carbon, hydrogen, oxygen, nitrogen, calcium, potassium, magnesium, sulphur, phosphorus, and iron — constitute a small fraction of the chemical elements known to exist, and they are only a few of the elements abundant and widely distributed in nature. Aluminum, for instance, is in all soils containing clay, silicon is in all soils containing sand. But, with the exception of sodium and chlorine, these ten elements occur in compounds more widely distributed than any others.

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[2] Bayliss, *l. c.*, p. 354.

[3] Pfeffer, W., *Handbook of Plant Physiology*. Transl. by Ewart, A. J., Vol. 1, p. 430, etc., Oxford, 1897.

Chemist and physical chemist may advance reasons as to why other elements than these ten are not indispensible to plants and animals, and as to the peculiar merits of these ten; but the question is still far from complete answer. The compounds of these ten elements fall into two groups, those which are volatilized and escape on combustion — carbon, hydrogen, oxygen, nitrogen, and those which form the ashes or ash, the persistent residue left on burning vegetable and animal matters. Ashes are made up of the oxides of calcium, potassium, magnesium, sulphur, phosphorus, and iron; but, in the soil and in solution in water, these elements are present as salts, as just pointed out. Furthermore, in dilute solutions, such as exist in the soil water and in the living cell, the elements may exist as ions or groups of ions along with compounds. The electrical, and other, properties of these ions may, by themselves, be beneficial to protoplasm, but as the ions of calcium or magnesium may be proved by experience to be damaging to protoplasm, so they may be conceived to be antagonistic to each other. Hence, if present in due proportions, they may render each other innocuous. Thus we have the idea of "balanced solutions" (see page 124). But while entertaining the modern idea of balanced solutions of alkaline ions we must not forget the more general and fundamental, and presumably more important, conception of the balance of alkaline and acid ions or radicles in all salts. Thus, just as the plant and animal cell has calcium and other alkaline ions to deal with in the course of its metabolism, so it has hydrogen ions also, and hence the flood of recent papers on hydrogen ion concentration,[4] the bearing and value of which are not at the present moment altogether clear. It is, however, obvious that, in the course of normal plant and animal metabolism, elements and compounds extremely dangerous in themselves are so dealt with that they not only do no damage but are indispensable. While specific uses, once assigned to each of the ten elements constituting the food materials and foods of living organisms,[5] cannot now be designated for them all, we know by experience that they must all be present in due amount, proportion, and form, if the organism is to flourish. Of the ten elements, the specific uses of carbon, hydrogen, oxygen, and nitrogen are the most evident, and it is their combination into substances directly usable as sources of material or energy for living cells that constitutes the most important question in physiology.

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[4] For a clear and concise statement of the conceptions concerning H-ion concentration see L. S. Medalia, "Color Standards" for the Colorimetric Measurement of H-ion Concentration, p. H 1.2 to p. H 9.8. *Journ. Bacteriology*, 5, 1920.

Fifty per cent of the dry weight of the bodies of plants and animals is carbon. The known physical and chemical properties of carbon help us to conceive reasons for this fact. These properties are summarized by van't Hoff[6] as quoted by Bayliss[7] as follows:

> 1. The quadrivalence renders possible an enormous number of derivatives of any one compound.
>
> 2. The capacity of carbon atoms of uniting with each other allows a great variety of modes of combination.
>
> 3. Its position in the periodic system, in the middle between positive and negative elements, gives it the power of uniting with the most different elements. . . . Owing to this, it is readily capable of alternate oxidation and reduction, and thus of acting as a carrier of energy.
>
> 4. When three of its valencies are saturated, the fourth valency

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[5] All the older textbooks made definite statements such as "Potassium is an essential for the assimilating activity of chlorophyll as iron for its production." (Sachs, J., *Textbook of Botany,* transl. by Bennett & Dyer, Oxford, 1875).

[6] Van't Hoff, J. H., *Ansichten über die organische Chemie.* 2 Bde, Braunschweig, 1881.

[7] Bayliss, W. M., *l. c.,* p. 41.

has a "positive" or "negative" character, according to the nature of the groups in the other three places.

5. The slowness of reaction or inertia of the carbon compounds is of much significance in vital phenomena.

This extremely valuable substance is obtained by all organisms directly or indirectly from the air, in which it exists as carbon dioxide in inexhaustible quantity and great dilution. The only organisms capable of taking carbon from the air are those able to break down carbon dioxide and water and recombine their components into sugar. The capacity of decomposing CO_2 and H_2O and of forming sugar is limited to those cells containing chlorophyll or its physiological equivalent, bacterio-purpurin.

The species, and even the individual cells, containing bacterio-purpurin are few, and their rôle in nature appears to be a very modest one. These "purple" bacteria seem to have received until recently[8] no special attention for a considerable time,[9] but their possible interest, both practical and theoretical, is so considerable that further studies, especially chemical ones, should yield valuable as well as interesting results.

Proof that the carbon-dioxide of the air, and not the organic matter of the soil, is the source of carbon for all living organisms is furnished by experiments made in almost every botanical laboratory, namely: (1) in which green land plants, cultivated in an atmosphere of normal composition, except that every trace of CO_2 has been removed, soon cease to grow and presently die; and (2) in which green land plants, cultivated in a soil of otherwise normal composition but containing no trace of carbon compounds, thrive perfectly. Corresponding experiments with submersed aquatics show that it is the CO_2

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[8] Becking, L., Studies on The Sulphur Bacteria. *Annals of Botany,* 39, 1925.

[9] Molisch, H., *Die Purpurbacterien.* Jena, 1907.

dissolved in water, and not sugar or other complex organic compound, out of which green plants make food.[10] The value, therefore, of loam, leafmold, manure, and other fertilizers, natural and artificial, is to be found not mainly or directly in their organic content, but rather in their indirect chemical effects and in their direct influence on the physical condition of the soil. Thus, soils containing due proportions of humus dry out less rapidly and completely than soils deficient in humus — a matter of great importance, and well understood, in the semi-arid portions of our far western states.[11] Furthermore, the living contents of the soil, the bacteria and fungi, are profoundly influenced by its organic contents and correspondingly affect the larger plants rooting among them. Proof of this is found in experience which teaches that sterilized humus is less useful than unsterilized. No doubt part of the difference is due to physical and chemical properties altered by the heat or other sterilizing agent; but part of the effect is also due to the death and consequent inaction of the micro-organisms. On the other hand, the spores or mycelia of dangerous parasitic fungi or bacteria may be carried in manure or other fertilizer, and the advantages of manuring may be more than offset by the infections which follow.

Granting that actual deficiencies in cultivated soil should be made up by the addition of suitable fertilizer, it is equally true, but not duly recognized, that much of the expenditure for fertilizer, and even in many instances for water, is uncalled for and wasteful if not injurious. Owing to the general aversion to manual labor on the part of the Anglo-Saxon population of this country, and the consequent high cost of other labor, agricultural and horticultural practice has favored the application of fertilizer and water rather than thorough tillage. The immediate result is no doubt satisfactory, but in the long run the soil deteriorates, accumulating salts of little or no value, losing in aeration and drainage. For adequate treatment of this extremely important subject, the interested student must turn to the writings of the agricultural and horticultural specialists,[12] bearing in mind, however, the fundamental principles of physiology in order to retain his general theoretical point of view.

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[10] Angelstein, A., *Untersuchungen über die Assimilation submerser Wasserpflanzen.* Dissertation, Halle, 1910. The suggestion is here made that the dissolved carbonates may serve as a source of CO_2.

[11] Russell, E. J., *The Fertility of the Soil.* Cambridge (England), 1913, p. 8, *et seq.*

The dilution of CO_2 in the air is extreme, the quantity enormous and, since approximately as much is restored to the air by respiration, etc., as is taken from it per annum, the supply is inexhaustible. Owing to the freedom of molecular movement of gases dissolved in gases, the supply of CO_2 is everywhere uniform and constant. That the supply has always been the same as now may not be true; for many suppose that the accumulations of coal, natural gas, and petroleum imply an atmosphere richer in CO_2 at the time that these measures were laid down than exists to-day. On the other hand, unless the rest of the machinery of living organisms were correspondingly different in past geologic time, a supposition as easy to make as any other, a higher proportion of CO_2 in the air would be more harmful than helpful. Furthermore, for the utilization of larger volumes of raw material larger amounts of energy would be required. Assuming the same sort and source of energy then as now, the earth must have received more sunlight in past geologic time. Perhaps it did; but of this so little is known that speculation is so easy as to offer small attraction. It is stated that the nearest living relatives of what appear to have been the predominant plants of the Carboniferous period, the ferns and their allies, are the plants best able to utilize increased amounts of CO_2 in light of greater intensity.[13]

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[12] Hilgard, E. W., *Soils, Their Formation, Properties, Composition, and Relations to Climate and Plant Growth in the Humid and Arid Regions.* New York and London, 1906. Molisch, H., *Pflanzenphysiologie als Theorie der Gärtnerei.* 4te Aufl., Jena, 1921.

Increase of the CO_2 content of the air has been advocated, especially in times of stress or because of special interest, in order to increase the yield of food in plot or greenhouse cultures. To insure the success of such experiments the adjustment of three fundamentally important factors must be favorable, other things being equal, namely, the supply of oxygen, water and other food materials; the supply of suitable energy; and the means of absorbing it. We can readily imagine that, in the cloudless atmosphere of the desert, an increase in the supply of CO_2, if accompanied by increased absorption of light by the chlorophyll pigments and adequate supply and conservation of water and other food materials, would result in increased food manufacture, but it is doubtful whether, in the cloudy regions of Europe, occupied by an industrial population, the attempt directly to utilize the CO_2 in factory smoke will succeed in accomplishing anything more important than temporary delusion of those interested.[14]

The proportion of CO_2 in ordinary air is between two and three hundredths of one per cent (0.02–3%). Calculating the amount of carbon in carbon-dioxide we have

$$\text{Atomic weight of } C = 12 \qquad C = 12$$
$$\text{Atomic weight of } O = 16 \qquad O_2 = \frac{32}{44}$$
$$C:CO_2 = 12:44 = 3:11 \quad 0.02 \times 3/11 = 0.005+$$

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[13] Godlewski, E., *Abhängigkeit der Sauerstoffausscheidung der Blätter von dem Kohlensäuregehalt der Luft*. Arb. a. d. Bot. Inst. in Würzburg, 1, 1874.

[14] See the papers cited in Botanical Abstracts, 8, p. 5 (No. 32), 1921, and earlier; also Fischer, H., in *Gartenflora,* 1919, and *Jahresb. d. Ver. f. ang. Bot.,* 11, 1913.

The proportion of carbon, therefore, in the air is 0.005%. This is an exceedingly small proportion to furnish the amount required, even by minute plants, unless we assume, as we must and easily may, the extremely rapid diffusion of CO_2 molecules through the air and absorption by living cells.[15] One half of any kilo, or pound, of dry weight of a plant body being carbon, we may calculate the amount of air from which all the CO_2 must be entirely removed, or realize the much larger volume from which a part of the CO_2 will be removed, in order to supply this amount of carbon, thus: 500 gr. or $\frac{1}{2}$ lb. of carbon = 0.005% of 5,000,000,000 cc. of air, or 4500 cubic yards of air are required to furnish a pound of carbon.

Granted a sufficient and persisting difference in the pressures of CO_2 inside and outside a living cell with membranes of usual composition, the flow of CO_2 will be adequate, according to the conditions discussed already; but not all cell membranes are permeable to CO_2. Hence we must examine this matter also. In multicellular organs, or multicellular organisms, living on land and between the tide-marks on the seacoast (*e.g.*, *Fucus*, *Laminaria*, etc.), the surface is formed by epidermal cells the outer walls of which are more or less heavily cutinized, becoming thereby impervious to water and water-solutes, including CO_2. If CO_2 is to reach carbon dioxide-absorbing cells in these organs or organisms in sufficient amounts, it must have, at times at least, free access to them from the air. In the case of land plants this is accomplished through the stomata,[16] while in the amphibious plants of the tidal zone the hairs of the "sterile conceptacles," etc. serve the same purpose.

While it will be necessary to study stomata from other points of view also (see pages 139 and 187), they should be considered now. They are openings through epidermis. These openings, in the case of the leaves of the usual land plants, are on the surface and somewhat more numerous on the lower than on the upper side of the leaf; but in this regard there is great difference, apparently according to circumstances as well as species. On the pendent leaves of *Eucalyptus globulus* ("blue gum" of Australia and California), the stomata are equal in number on the two similar sides.[17] The relations of light, humidity, and other factors of the environment to the formation and the distribution of stomata will be further discussed in the following pages (139, 296, 336). Suffice it to say here that plants of the shade, where the air tends also to be damper, have stomata more nearly equal in number on the upper and lower surfaces, whereas plants of the open have stomata mainly or entirely on the side away from the light. In the case of desert plants, the stomata are not superficial, but are sunk in grooves or pits in the very heavily cutinized epidermis.

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[15] Spoehr, H. A., and McGee, J. M., Absorption of Carbon Dioxide the First Step in Photosynthesis. *Science*, 59, 513–4, 1924.

[16] Stahl, E., Einige Versuche über Transpiration und Assimilation. *Bot. Zeitung*, 52, 1894.

In a considerable number of plants, generally speaking those living where there is a uniformly ample supply of water, as for example willows, the stomata which, in other plants, are opened and closed by the expansions and contractions of the so-called guard-cells, remain constantly open, the guard-cells being incapable of change of form. From this it might be inferred that stomata are mainly for the control of water loss by evaporation. This conclusion would be erroneous, as the observations of Gray and Peirce[18] show; for mere dryness or moistness alone of the air or of the soil will not induce the stomata to close or open; whereas, even if the air or the soil is dry, the stomata will open in sufficiently bright light, and will close even in damp air or if the soil is moist when the light dims sufficiently, as indicated by direct microscopic observation of the undisturbed stomata of live whole leaves in place. It may be claimed for these observations, if correct, that they are less likely to indicate other than actual conditions in the living organisms than methods, however ingenious, which involve on the one hand either unnatural mechanical or chemical treatments of living cells, tissues, or organs, or on the other the artificial models of living things. It is not intended to imply that such methods and models have no place, but that they should have their proper place rather than the whole place in physiological laboratories and investigations; for, after all, we should be studying the live thing rather than any array of models under whatever name they may pass at the moment.

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[17] The same is doubtless true of other plants with pendent leaves and of those "compass" plants the leaves of which are erect. The distribution of stomata in the epidermis of the rounder needles of the pines, as compared with the flatter ones of the firs, is nearly uniform on all sides.

[18] Gray, J., and Peirce, G. J., The Influence of Light upon the Action of Stomata and its Relation to the Transpiration of certain Grains. *Am.*

The passage of CO_2 through cutinized epidermis, shown to be very slow by Stahl's experiments[19] in closing the stomata by coco-butter or other fat, takes place through the open stomata by diffusion, the air in the intercellular spaces of the leaf being continuous with the air outside whenever the stomata are open. While it has not been shown that the amount and quality of light in which stomata open is the same as that of photosynthesis, experiments have sufficiently proved that light controls both, so that it is obvious that the two processes are very closely and suitably linked together.

Jour. Bot., 6, 1919. See also Darwin, F., On the Relation between Transpiration and Stomatal Aperture. *Philos. Trans.*, London, ser. B 207, 1916. Lloyd, F. E., The Physiology of Stomata. *Carnegie Inst., Wash., Pub.*, 82, 1908. Briggs, L. J., and Shantz, H. L., Relative Water Requirements of Plants. *Journ. Agric. Research*, 3, 1914.

[19] Stahl, E., *loc. cit.*

The size, number, position, and openness of stomata vary, as we have seen, with the species, the environment, and the stimulus, light. That they furnish sufficient entrance to CO_2, even in thick and heavily cutinized leaves, with much chlorophyll-containing tissue, and in strong illumination, is shown, for example, by examination of orange leaves late in the day. Other conditions being suitable, their mesophyll cells will contain great quantities of starch, in spite of the fact that in those leaves the stomata, limited to the under side, are neither large nor remarkably numerous. In thinner, less heavily cutinized leaves, exposed to less light in the more humid parts of the north temperate zone, where such studies have, for the most part, been carried on, the classical experiments of Sachs[20] and the very thorough investigations of H. T. Brown and his associates[21] have shown that starch, formed by fixing CO_2 in chlorophyll-containing cells, accumulates in leaves throughout the daylight hours and is ordinarily most abundant at sundown. The carbon-dioxide, unable to enter through the cutinized epidermis, diffuses freely through the stomata when they are open. These openings occupy varying fractions of the total leaf surface,[22] from one to fifty per cent. But it is well known that, under equal pressure, gases and liquids will flow relatively more rapidly through small than through large openings. This is the principle employed in all pipes, faucets, nozzles, etc. Thus, Brown has shown that the smaller the opening the more rapid the diffusion through it.

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[20] Sachs, J., *Ein Beitrag zur Kenntniss der Ernährungstätigkeit der Blätter*. Arbeit. bot. Inst. Würzburg, 3, 1884; Ges. Abhandl., 1, 1892.

[21] Brown, H. T., The Fixation of Carbon by Plants. *Nature*, London, 1899. Brown, H. T., and Morris, G. H., A Contribution to the Chemistry of Foliage Leaves. *Journ. Chem. Soc.*, London, 1893. Brown, H. T., and Escombe, F., Static Diffusion of Gases and Liquids in Relation to the Assimilation of Carbon and Translocation in Plants. *Trans. Roy. Soc.*, Series B, 193, London, 1900. Researches on Some of the Physiological Processes of Green Leaves. *Proc. Roy. Soc.*, Series B, 76, London, 1905.

[22] Pfeffer, W., *Handbook of Plant Physiology*, Transl. by Ewart, I, p. 195. Oxford, 1900–03.

This inward diffusion through stomata into the intercellular leaf spaces will vary with the rate of fixation of CO_2 in the chlorophyll-containing cells, being necessarily most rapid at the time of maximum illumination and varying from day to day and place to place with the amount of light. The rate of CO_2 diffusion will, therefore, depend upon the difference between the usual proportion of CO_2 in the outside air and the less or none in the air inside the leaf. How rapid this may be can be shown to the eye by exposing a strong aqueous solution of barium hydroxide to the air and noting how quickly a visible film of barium carbonate forms on the surface of the liquid.

Photosynthesis and Chlorophyll

The continued diffusion of CO_2 into the interior of leaves implies, among other things, the continued removal of CO_2 as such from the leaf, the maintenance of a gradient down which CO_2 molecules roll. The removal of CO_2 is accomplished by decomposing its molecules and the molecules of water and recombining their constituents. This process, called photosynthesis,[23] implies the application of energy in doing the work indicated. Obviously this energy must come from outside; it too must be " absorbed." Man set up various means to " absorb " energy, sails to catch the wind, wheels to convert the flow of water into usable power, photographic and electric appliances to use light and electrical energy. The photographic plate contains silver or other salts which, stable in the dark, are readily decomposed by light. The energy absorbed by the salts splits the acid radicle from the metal, which is precipitated as such. Color screens of various sorts employed in photography absorb the corresponding rays of light before they can reach the plate, and accordingly influence the changes taking place therein. The green leaf is precisely a system of color screens by means of which light rays of certain wavelengths are absorbed. The pigments forming these color screens are known as chlorophyll. They occur inside living cells and, in all but the lowest plants, in definitely recognizable bodies, chromatophores. Because of the shape of many chromatophores, they are commonly spoken of as chlorophyll grains, though the pigments themselves may exist in the chromatophores in the colloidal condition.[24] The chlorophyll pigments, which give the usual green color to leaves, may themselves be masked by other pigments contained either in solution in the cell sap, or in the chromatophores (see pages 59–75). Of course white parts of leaves, etc., like white hairs on animals, owe their whiteness to the total reflection of light from the air-filled cells of the surface of the white objects.

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[23] See Barnes, C. R., On the Food of Green Plants, *Bot. Gaz.*, 18, 1893, who proposed the word photosyntax. The term photosynthesis has now come to be generally used as implying the synthetic change taking place in the green leaf. But Schroeder, H., in his painstaking and valuable summary, *Die Hypothesen über chemischen Vorgänge bei der Kohlensäureassimilation und ihre Grundlagen* (Jena, 1917), not only retains the expression carbon assimilation, now for the most part discarded by English-speaking physiologists, but proposes (p. 1) *photoenergetic* in place of *photosynthetic* activity, in the process of food manufacture, on the ground that we know that light is the source of energy used but that we do not know that it acts as light in the synthetic process. This is an entirely valid distinction.

The green of leaves has long been a subject of the most able and acute investigations, with results which leave us regrettably far from full explanations. The literature of the

[24] K. Stern, in the *Zeitschr. f. Bot.*, 13ter Jahrg., 1921 (Ueber die Fluorescenz des Chlorophylls und ihre Bedeutung beim Assimilationsprozess), claims, on the basis of spectroscopic and ultramicroscopic investigation, that the pigments are in actual solution. He considers that the " chloroplast is an emulsion-colloid or an emulsion of chlorophyll-lipoid and hydroid-plasmatic substance."

subject is so extensive, and so much of the work is now of historical interest mainly that it need not be reviewed here.[25] The most comprehensive as well as penetrating and thorough work has been done in recent years by Willstätter and his associates,[26] who have added greatly to our knowledge of the chemistry of the pigments. On the basis of this, progress toward a knowledge of the chemical process of food manufacture may be hoped for, though perhaps not yet expected. It must still be feared, in spite of the great superiority of Willstätter's methods over those of his predecessors, that we do not yet know the composition of the pigments as they actually exist in the chromatophores of living cells. Chemical methods still involve treatment by extractives and other reagents in themselves fatal to living things; and we have long known enough about the chlorophyll pigments to be very certain of their sensitiveness and instability in the presence of active reagents, whether free acid, alkali, or other substances, even in such dilute solution as the cell sap.[27] Hence it is almost necessary to suspect that Willstätter's chlorophylls are derivatives rather than the pigments of the living cells.

From Willstätter's extract of dried nettle leaves in acetone, four pigments may be separated, Chlorophyll *a* and Chlorophyll *b*, the one bluish green in solution, the other yellower green, respectively, the former being the more abundant and the more sensitive to acids; and Carotin and Xanthophyll, yellow in color. Analysis shows no nitrogen in the last two substances, but that it is present, with magnesium, in chlorophyll *a* and *b*. From four kilos of fresh leaves dried down to one kilo the following amounts of chlorophyll pigments were extracted:

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[25] Consult for bibliography, Pfeffer, *Physiology*, Eng. Transl. by Ewart.

[26] Willstätter, R., and Stoll, A., *Untersuchungen über Chlorophyll*, Berlin, 1913. A valuable abstract in English by Jorgensen, I., and Stiles, W., was published in the *New Phytologist*, 14–16, 1915, and is obtainable as a separate pamphlet under the title of "Carbon Assimilation, a Review of Recent Work on the Pigments of the Green Leaf and the Processes Connected with Them." See also Wilstätter and Stoll, *Untersuchungen über die Assimilation der Kohlensäure*, Berlin, 1918.

[27] It may well be that the next steps in our progress toward a knowledge of the chlorophyll pigments will be made with the aid of physical apparatus applied to the living leaves or cells, as suggested by Stern, *loc. cit.*

Chlorophyll *a*	6.22 gr.
Chlorophyll *b*	2.26 “
Carotin	0.55 “
Xanthophyll	0.93 “

These are not inconsiderable quantities, and it is to be expected that reinvestigation of the subject of the amounts of chlorophyll in different plants in different environments, using Willstätter's or even better methods, will show, contrary to the positive statements of earlier authors, that the amounts vary considerably and in accordance with circumstances. The reasons for such expectation are the differences in the quantities of food made in the leaves of different species, differences in the shade of green, and finally differences in the amounts and qualities of light available in different regions, together with the accompanying differences in structure of the leaves. It may well be that the different species of herbaceous plants living in the same open field have approximately the same amounts of chlorophyll per cell or per unit of leaf area; but it does not seem reasonable that plants of the open should have the same quantities as those of the shade, and that those of intensely insolated regions, like Southern California, Arizona, and other arid or semi-arid regions, should not differ in this, as in other respects, from the more familiar plants of more humid and hence less lighted regions. The dark green of the foliage of orange and other citrous trees, with their double palisade layer and their mesophyll cells abundantly supplied with dark chromatophores, more than suggest that they have more chlorophyll per leaf area than the gray-haired sage brush which may live beside them. However, this question, and others relating to the proportions of the different chlorophyll components, can be answered only by thorough chemical investigation of many species living under very different conditions. As I shall have occasion to point out later (pages 223–349), most experimental investigation of environmental differences has been limited by the inability of the investigator to secure for his experiments essentially different conditions, and by our only too general inability to realize the great diversity of conditions prevailing over different parts of the earth's surface. Living in a well-watered feebly illuminated region, one may not realize the brilliant sunshine of Italy and Greece, perhaps still less the conditions in different parts of our own country.

The relation of the component pigments of chlorophyll to those color changes regularly taking place in nature, and occasionally occurring through man's interference with nature (see pages 61–2), should be considered, but, from what has already been said, it is evident that definite knowledge is not now possible. The autumn coloring, for which New England and the northern tier of states east of the Rocky Mountains are justly famous, and which develops principally in the foliage of maples, elms, and oaks, is due in part to the withdrawal from the leaves, or the destruction therein, of the pigments which Willstätter calls chlorophyll *a* and *b*. The relative proportions of the still persisting carotin and xanthophyll, and of the supplementary water-soluble pigments, if any, in the cell-sap, together with such total reflection of light as may take place from dead and air-filled epidermal cells, combine to produce the yellows, reds, and bronzes of autumn.

Color changes are really very common and are not limited to any particular season, although the main display may occur, by reason of climatic conditions, at some one time. There are gorgeous leaves in the tropics as well as in temperate lands, in aquatic as well as land plants, in spring and summer as well as in the fall, and in certain regions the oaks retain their bronze-hued dead leaves throughout the greater part of the winter. Beds of *Azolla,* for example, take on wonderful crimson shades in early summer on the pools of streams which stop during the dry season of California; and the *Salicornias* on the flat shores of San Francisco Bay offer some compensation in summer and fall for the general lack of autumn coloring in the landscape of the far West. The summer leaf-fall, to which Wiesner called attention years ago,[28] is preceded by color-changes which closely resemble those of autumn.

The color-changes are affected, if not brought about, by changes in the light, temperature, and water relations of the plants concerned. The color-changes occur in plants so diverse, living under conditions so different from each other, that no brief general statement regarding their causes can be made. For example, temperature and light probably influence *Azolla* and *Salicornia* more than differences in water relations in taking on a color which masks their greenness. In this respect there is an essential difference from the color-changes in leaves about to die, and also from those which occur in certain coniferous evergreens during and after winter cold,[29] *e.g.*, in arbor vitæ and its garden relatives, in which in cold weather bronze rather than green shades predominate. It has been claimed that these changes in color are due as much to light as to cold, but convincing experimental evidence is still lacking and, now that we know somewhat more of the liberation of heat within the cell, we may be the more inclined to suspect that the persistent greenness of the so-called more shaded parts of the foliage is due rather to their less exposed and therefore somewhat warmer position.

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[28] Wiesner, J., Ueber Laubfall infolge Sinkens des absoluten Lichtgenusses (Sommerlaubfall). *Ber. d. deutschen. Bot. Ges.*, 24, 1904. Also *Biologie der Pflanzen,* 3te Aufl. 3, pp. 924, 1913.

[29] Batalin, A., Ueber die Zerstörung des Chlorophylls in lebenden Organen. *Bot. Zeitung,* 32, 1874.

The persistent greenness of winter wheat and of a considerable number of other plants under conditions completely destructive of the pigments, and even the cells and organs, of other plants similarly situated, may reasonably awaken doubt both as to the proportions and even the identity of the chlorophyll pigments in all plants. This remark, by one who makes no pretense of being a chemist, implies no criticism of the results of the remarkable work of Willstätter and his associates, but only renews the query whether, after all, their researches were carried out on derivatives rather than on the pigments actually existing and working in living cells. In fact, the extraordinary sensitiveness of the chlorophyll pigments of some plants, and the relative immunity of others, is a phenomenon familiar to those botanists acquainted in any degree with the effects of injurious gases and vapors upon different plants. I am comparatively unfamiliar with the harmful effects of tar vapor, but there are many instances, recorded and unrecorded, of injury to adjacent plants from the "steam" from hot tar, whether applied to road, roof, or masonry wall; or merely being heated in a kettle on the ground. On the other hand, extensive experience with sulphur fumes has shown me certain remarkable results, examples of which may be mentioned. On the bare hills of the upper Sacramento Valley in California, the only plant showing no macroscopic evidence, in change of color or otherwise, of the effect of the sulphur dioxide at one time discharged without restriction from the smelters of the region, was "poison oak," *Rhus diversiloba*. Everything else was discolored, corroded, or dead. Similarly, on one occasion, I noted that the plant which showed no evidence of injury, but on the contrary throve to such a degree as to be a pest, in the hay fields about Anaconda, Montana, was the common dandelion, *Taraxicum densleonis*. The various kinds of cultivated beans, on the contrary, are so sensitive that they cannot be grown in some "smoky regions," their leaves showing abnormal coloring, spots, and corrosions at the same time that other plants by their side in the same garden appear normal. Beans are in fact taken as "indicator plants" by students of smelter injury.[30] In view of these facts it is easy to guess that one reason for the diversity in autumn coloring is the original diversity of pigments in the leaves.

That not merely temperature and light changes, as such, affect the colors of leaves before their fall, is obvious to one who realizes that temperature changes induce other changes in the environment as well as in the organism. Thus a rise or fall in temperature will alter the water relations of every living thing on the land area affected. It will regulate the rate of evaporation not only because evaporation varies with the temperature, other things being equal, but because the water-absorbing capacity of the air also varies with its temperature. It will regulate the rate of absorption because roots absorb more and more slowly as the soil temperature falls, and from frozen soil there may be no absorption of water while evaporation continues into the air (see page 337). We thus have effects on the chlorophyll pigments primarily due to changes in temperature, but the direct results of the proportions of water in the cells. It may be wondered, therefore, if some of the winter changes previously discussed (pages 60–1) may not be due in part, or in certain instances, to changes in the proportions of water in the chlorophyll-containing cells of the "rusting" foliage. Further investigation is required to satisfy curiosity on this point.

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[30] For the extensive literature of this subject see the *Report of the Selby Smelter Commission.* Bull. 98, U. S. Bureau of Mines, Washington, 1915.

Deciduous leaved plants generally protect themselves against open wounds by the formation of a so-called abscission layer at the base of the petiole of a leaf about to fall. The time and manner of formation, as well as the structure of these cork septa which develop in different species, even of herbaceous plants, have been extensively studied (see pages 286–289), as may be seen from the literature.[31]

In this connection it may be stated, although the subject will be examined later (see page 337), that some cases of so-called "winter killing" are not at all the consequence of extreme cold, for there need be none; but if evaporation be rapid, as for example when the air is dry, the wind high, and the plant not well insulated by cork or cutin, while the ground is nearly or quite frozen, the plant will dry out correspondingly fast and die. The different degrees of tenderness to cold, as indicated by color changes and other differences in appearance, also suggest differences in the chlorophyll pigments of different plants in spite of current evidence to the contrary.

The chlorophyll pigments, diffused in the lowest algæ throughout the cytoplasm,[32] and confined in all other green plants to chromatophores of different shapes and sizes, are placed by the movements of the organism or the organ or the chromatophores themselves in the path of the incident rays of light (see pages 320–321). In unicellular plants the position of the plant determines whether the cell will receive sufficient light, whereas in multicellular plants only those cells on or near the surface of the mass can receive any considerable amount of light. In the large multicellular plants of land and sea (*Fucus*, *Laminaria*, the great kelps, etc.) the chromatophores are fully developed only in cells on or near the surface both of the water and of the plant, and, if the relations to water permit, in parts of the plant body expanded into organs more or less flat. The most compact plants of the Arizona desert, the cacti, for example, have no leaf-like organs owing to the dryness of the soil and the low humidity of the air through long seasons. Otherwise, land plants have leaves or are themselves leaf-like. The area, thickness, structure, arrangement and position of the leaves is largely a matter of circumstances to be discussed later; but it should be pointed out at once that the relation of leaves to CO_2 and light are directly opposed to the relations to water supply and water loss. Any area, structure, and disposition of leaves facilitating access of CO_2 and light will also facilitate water loss without correspondingly increasing water supply. Hence the leaf of any given plant, while more or less fixed by heredity, is also the resultant of these two opposing influences. In the works of plant geographers[33] and ecologists[34] descriptions of the foliage of the land plants of different regions will sufficiently illustrate this matter.

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[31] See Goodspeed, T. H., and Kendall, J. N., An Account of the Mode of Floral Abscission in the F. Species Hybrids of Nicotiana. *Univ. Calif. Publ. Bot.*, 5, 1916. Kendall, J. N., Abscission of Flowers and Fruits in the Solanaceæ. *Ibid.*, 5, 1918. Hodgson, R. W., An Account of the Mode of Foliar Abscission in Citrus. *Ibid.*, 6, 1918, and the literature therein cited.

[32] Wager, H., The Cell Structure of the Cyanophyceæ, Prelim. paper. *Proc. Roy. Soc.*, London, 72, 1903.

If leaves or other parts of the plant body look green it is because they absorb those rays of light which would otherwise reach the eye of the beholder. Light is a form of energy. If light is absorbed by any object, it will change the temperature of the object, or accomplish work of some other sort, or both. Hence leaves, or rather the green cells in them, as organs for absorbing CO_2, are also organs for absorbing energy. Spectroscopic examination of leaves and of solutions of the pigments extracted from them show very definite relations to light. The spectra differ according to the but indefinitely known quantities of chlorophyll examined. Thus no one knows the amount of chlorophyll in the living nettle leaf, the spectrum of which is figured, for example, by Willstätter and Stoll,[35] who give, for comparison, the spectra of an alcoholic extract and of solutions of the chlorophyll components.

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[33] Schimper, A. F. W., *Plant Geography*. Eng. transl. by W. R. Fisher, Oxford, 1903.

[34] Cowles, H. C., Ecology. In *Textbook of Botany*, by Coulter, Barnes, and Cowles, New York, 1911. Clements, F. E., Plant Physiology and Ecology, New York, 1907.

Certain pronounced absorption bands in these spectra fix the attention, the principal one being in the red, the less striking one in the violet. The importance of these bands, and of the other much fainter ones, is directly in proportion to their intensity so far as experimental evidence indicates. Sachs,[36] on the basis of his well-known experiment with colored bell-jars, concluded that the rays in the red, or as he supposed in the yellow, were the most effective. But as pointed out by many critics, the quantities of energy received by plants under Sachs's potassium dichromate solutions were considerably greater than those under the cuprammonium solutions. Kniep and Minder[37] showed experimentally that the amounts of starch and sugar made in lights of different colors are about proportional to the amounts of energy absorbed by the red and the violet parts of the spectrum. The classical experiments of this sort were made by Engelmann[38] who threw a spectrum upon a *Cladophora* filament in water in which were also numerous motile bacteria chemotactic to oxygen. As reported by Engelmann, the bacteria gathered in largest number in the upper red, between the Frauenhofer lines B and C, a second and minor gathering place being in the violet near the line F.

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[35] Willstätter and Stoll, *Untersuchungen über Chlorophyll*, p. 62.

[36] Sachs, J., Wirkungen farbigen Lichts auf Pflanzen, *Bot. Zeitung*, 1864. Gesammelte Abhandlungen 1, 261, 1892.

[37] Kniep, H., and Minder, F., Ueber den Einfluss verschieden farbigen Lichtes auf die Kohlensäureassimilation. *Zeitschr. Bot.*, 1, 1909.

[38] Engelmann, T. W., Ueber Sauerstoffausscheidung von Pflanzenzellen im Mikrospektrum. *Bot. Zeitung*, 40, 1882.

One may draw either of two inferences from the foregoing experiments on photosynthesis, either that the rays absorbed are, because of their wave-length, the ones most effective in one or another stage of the process, or that, as suggested above, the effectiveness of the different rays (colors) is proportional merely or mainly to their amount. In weighing the respective merits of these two inferences one is greatly hampered by not knowing exactly the course of the chemical changes taking place in or on the chromatophore. It is obvious that one or both of two saturated and extraordinarily stable compounds, CO_2 and H_2O, which are torn to pieces only with difficulty in the laboratory, are reduced and recombined into compounds which though fairly stable, dry and in the air, are unsaturated and very easily acted upon by many agents under the conditions prevailing in living cells. The equation representing the extremes of this series of chemical changes is

$$6\ CO_2 + 6\ H_2O = C_6H_{12}O_6 + 6\ O_2$$

Inspection of these symbols shows that in the carbohydrate, grape sugar, the hydrogen and oxygen are in the same proportions as in water, as is implied by the name carbohydrate. From this one might guess that only the CO_2 was split and that the thus unengaged carbon became attached to an H_2O molecule; but does our acquaintance with carbon and water encourage such an hypothesis? Experience would lead rather to the inference that the H_2O is split as well as the CO_2. Some of the O_2 released may, therefore, come from CO_2 and some from H_2O molecules.

In the next place, while CO_2 and H_2O can be made to enter into unstable combination as carbonic acid H_2CO_3, from which certain carbonates can undoubtedly be made, it is not the starting point of a series of compounds at all nutritious in the ordinary sense or to most organisms. On the other hand, the atoms of carbon, hydrogen, and oxygen can be combined under certain conditions into formic acid, CH_2O_2, and this reduced to formic aldehyde CH_2O, which can be made to polymerize, becoming $C_6H_{12}O_6$ or some other hexose sugar, possibly by way of the pentoses. This is the famous hypothesis of von Baeyer [39] in barest outline with the addition of the pentoses discovered by Spoehr [40] to be abundant and considered by him in connection with the problems of sugar synthesis both inside the cell and outside. The remarkable work of Emil Fischer [41] on the sugar group, by means of which the rapidly accumulating mass of facts was given orderly arrangement and the existence of the whole series of sugars and their derivatives was demonstrated, gave support to von Baeyer's hypothesis, which has been still further strengthened from the chemical side by the work of Stoklasa and his school.[42] Miss Baker [43] and many others, references to whose work will be found in the papers already cited, have shown that under special conditions, salts of formic acid, formaldehyde, and derivatives of the latter, can be utilized by certain plants as sources of sugar and starch. It may be said of all these investigations, extremely interesting and valuable though they undoubtedly are, that they have not justified belief that we know very much about what goes on every day under our eyes in every green cell! The great work of the chemists has by no means been equalled by botanists, who either have been unable to make use of what the chemists have given them, or have been baffled by the difficulties of handling, in connection with living cells, the extremely poisonous formic acid and formic aldehyde and the reagents required in dealing with them.

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[39] Baeyer, A. von, Ueber die Wasserentziehung und ihre Bedeutung für das Pflanzenleben und die Gährung. *Chem. Ber.*, 3, 1870.

[40] Spoehr, H. A., Theories of Photosynthesis. *Plant World*, 19, 1916. See also Schroeder, H., *Die Hypothesen über die chemischen Vorgänge bei der Kohlensäure assimilation und ihre Grundlagen*, Jena, 1917.

[41] Fisher, E., *Untersuchungen über Kohlenhydrate und Fermente.* Berlin, 1919.

[42] Stoklasa, J., and Zdobnicky, W., Photochemische Synthese der Kohlenhydrate aus Kohlensäureanhybrid und Wassestoff in Abwesenheit von Chlorophyll. *Biochem. Zeitschr.*, 30, 1911.

[43] Baker, Sarah M., Quantitative Experiments on the Effect of Formaldehyde upon Living Plants. *Ann. Bot.*, 27, 1913.

It goes without saying that chemical glassware, as well as the apparatus of the physical-chemist, is vastly different from the living cell, and great caution should be observed in stating the results of researches under one set of conditions as the facts of nature. While plants, as well as human society, can be forced to survive on “ Ersatzmitteln ” of various sorts, no one will wish to claim that substitutes for foods are as satisfactory as the foods themselves.

On the other hand, the series of experiments reported by Benjamin Moore and his associate Webster,[44] terminated by the regretable death of the former, deserve careful consideration. These bio-chemists proceeded with admirable caution and enviable skill in their studies extending over a period of years. As cited above, their work began with an examination of the behavior of living cells in relation to the synthesis of food from inorganic materials. Whatever interest we may or may not have in speculations about evolutionary history or relationships, it is logically necessary to conceive either that the chlorophyll-containing cell was created able to nourish itself and other living cells, or that it developed this ability from a beginning extremely simple and limited. The biologist and the chemist of to-day naturally imagine a simple colloidal system operated with energy absorbed from outside itself and most naturally by light as the commonest and most available source. Hence Moore and Webster's use of a system of colloidal iron exposed to light, CO_2, and H_2O. In this they presently found formaldehyde in appreciable amounts. It has long been a mystery why iron, though not a constituent of the chlorophyll pigments, seemed to be indispensable to their formation. The older explanations, which will be found recounted in Pfeffer's *Plant Physiology*,[45] are impressively lame or worse. Only further work will show whether Moore and Webster are justified in describing the chlorophyll granule as a mass of colloidal iron on or near the surface of which the chlorophyll pigments are spread. Granting that colloidal iron may by itself effect the synthesis of formaldehyde by using the energy in sunlight, it is obvious that formaldehyde found in a cell must be immediately made innocuous or the cell will suffer or die, and that the work can be done only with the expenditure of more energy, more than will be absorbed by a minute system of colloidal iron. According to the hypothesis of von Baeyer,[46] formaldehyde by polymerizing is rendered harmless as rapidly as it is formed. The end of this series of polymerizations is some hexose sugar.

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[44] Moore, Benj., and Webster, T. A., Synthesis by sunlight in relation to the origin of life. Synthesis of formaldehyde from carbon dioxide and water by inorganic colloids acting as transformers of light energy. The presence of inorganic iron compounds on the chloroplasts of the green cells of plants, considered in relationship to natural photosynthesis and the origin of life. *Proc. Roy. Soc.*, London, Series B, 87, pp. 163 and 556, 1913–14. Action of light rays on inorganic compounds and the photosynthesis of organic from inorganic compounds in the presence of inorganic colloids. *Proc. Roy. Soc.*, London, Series B, 90, 1917–19. Studies of photosynthesis in fresh water algæ. (Studies of marine algæ promised later.) *Proc. Roy. Soc.*, London, Series B, 91, 1920.

According to Moore and Webster, therefore, the function of

[45] Pfeffer, W., transl. by Ewart, A. F., pp. 426.

[46] *Loc. cit.*

chlorophyll is to absorb or transform the absorbed energy to effect the polymerization of the formaldehyde, already formed from CO_2 and H_2O in the colloidal iron system of the stroma of the chlorophyll grain. The iron is needed for the stroma rather than for the pigments incorporated with it, and the two, the iron and the pigments, accomplish the photosynthesis of sugar from CO_2 and H_2O. This hypothesis, as well as von Baeyer's, is strengthened by the experiments on unicellular fresh water algæ which Moore and Webster conducted in glass flasks favorably placed in a lawn in pure air during the summer months. They assert that in flasks sealed from the CO_2 of the air, supplied very gradually and in great dilution with formaldehyde or methyl alcohol vapors, respectively, they found a substantial gain in the carbon content. Thus, for the first time, as they believed, they have demonstrated the use, by green plants, of formaldehyde, and not a derivative,[47] under conditions departing from the normal as slightly as possible in every particular, except the deprivation of CO_2.

The somewhat similar, and from the botanists' point of view less satisfactory and encouraging investigations of Baly,[48] begun before Moore's death and continued since, while confirming and extending our knowledge of the capacity of formic aldehyde to polymerize to a hexose sugar or to some other compound, throw little, or indeed no, light upon the fundamental question of how the first combination of carbon and water is accomplished. To chemist and biologist alike this is the most important problem of all: its solution may free man from his dependence upon the present sources of food: it may make him actually independent, actually free, the freest creature in all Nature instead of one of the most dependent.

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[47] See Loew, O., Ernährung von Pflanzenzellen mit Formaldehyd. *Bot. Centralb.*, 44, 1890. Bokorny, Th., Ueber Stärkebildung aus Formaldehyd. *Ber. d. Deutsch. Bot. Ges.*, 9, 1891; *Biolog. Centralb.*, 17, 1897.

[48] Baly, E. C. C., Heilbron, I. M., Stern, H. J., Photocatalysis. *Journ. Chem. Soc.*, London, 1923 and preceding.

In a brief paper,[49] to be followed by fuller statement later, Spoehr and his associate McGee give some results of their investigation of the fixation of atmospheric CO_2 by the constituents of chlorophyll-containing cells. They find that by treating dried sunflower (*Helianthus annuus*) leaves with water saturated at 20° C. with ether, and evaporating the extract at 50° C. to dryness they obtained a residue mainly protein which absorbed as much CO_2 per unit of time and mass as the "fresh leaf material." This dried residue constituted about 15% of the fresh leaf. Its capacity for absorbing CO_2 is similar to that of the venous blood of human beings, and many times greater than that of water. Presumably then, the CO_2 is loosely bound to some protein molecule or molecules as it is bound in venous blood to hæmoglobin; and from these are split off, under suitable conditions of illumination, etc., the asymmetric carbohydrates formed in the photosynthetically active cells of green plants. No formaldehyde or carbonic acid would be expected, under these conditions, nor did Spoehr and McGee find any. This, then, presenting the first new view in regard to the means of forming sugar in green plants, is the first contribution to the subject presenting anything more tangible in opposition to the hypothesis of von Baeyer than opinion and prejudice. It may be an exceedingly important contribution.

The fluorescence of chlorophyll solutions and of chlorophyll in the living cell, strikingly characteristic of them, has been investigated and described repeatedly but without definitely connecting this phenomenon with the manufacture of food. The general phenomenon of fluorescence consists in the absorption of light and its radiation at the same or other wave-length. Presumably radiation and absorption are not equal, and therefore energy may be available for chemical work. In the case of chlorophyll, assuming that the chlorophyll pigments as they exist in living cells have the same fluorescence as the solutions containing leaf extracts,[50] the change in the wave-length may make some of the light usable which would otherwise be useless or possibly harmful (ultra-violet-rays?). There is, in this subject, ample room for investigation, the results of which cannot fail to be of both value and interest.

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[49] Spoehr, H. A., and McGee, J. M., Absorption of Carbon Dioxide the First Step in Photosynthesis. *Science*, 59, pp. 513–14, 1924.

Other Pigments

In addition to the pigments giving greenness to leaves, young stems, etc., one commonly sees in nature and in cultivation other colors, only some of which are derivatives of the chlorophyll pigments, the others being distinct both in composition and behavior. Ascending the series in current classifications, from the so-called "purple" bacteria (see page 214) with their bacterio-purpurin which completely masks the chlorophyll which Molisch asserts they possess, and the other pigments made by bacteria but not concerned in food manufacture, we find the algæ named according to their colors, the blue-green (*Cyanophyceæ*), the brown (*Phæophyceæ*), the red (*Rhodophyceæ*), in all of which there are pigments supplementary to chlorophyll and masking it. Similarly in higher plants we find, as in the leaves of *Coleus, Amaranthus,* etc., red pigments dissolved in the cell-sap. The leaves of many plants as they come out in spring are red, becoming later green through the disappearance of the red coloring matters from the epidermal cells. These various pigments have been subjected to chemical and other investigations which are summarized, and the literature of which is cited in the publications named in the following paragraphs.

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[50] This is asserted by Stern, Ueber die Fluorescenz des Chlorophylls, *Zeitsch. f. Bot.,* 13, p. 227, 1921.

The blue-green algæ, many of which are olive or bronze rather than blue-green, contain a pigment or pigments soluble in water. This coloring matter may be extracted on grinding a mass of *Oscillatoria, Nostoc,* or other cyanophyceous plants in distilled water. The filtered extract is light blue in color. The pigment called phycocyanin may be crystallized out as dark blue bodies. These consist of one or more protein-like compounds.[51] From the mass left on the filter alcoholic extract of the chlorophyll pigments can readily be made.

The significance of this blue pigment is not now known. Reasons for our ignorance are obvious; for, besides the great range in color, from bright green to almost black, which one finds among the *Cyanophyceæ,* the conditions under which they live are widely different. Thus, we find them in waters extremely cold and very hot, in places only irregularly moistened and for much of the time intensely illuminated, in others constantly wet and dimly lighted, where the water is of extraordinary purity, and where it carries a load of dissolved organic matter often of most unpleasant origin. We cannot conceive of the same pigment as screening the chlorophyll and protoplasm from excessive light in one situation and supplementing the meager supply of light in another; and we do not know what part, if any, the rays absorbed by this blue pigment in dilute solution in water take in the chemical changes accomplished in the protoplasm. For in the *Cyanophyceæ* the chromatophores are more rudimentary or at least less differentiated than in the higher algæ and hence we know still less about the disposition of chlorophyll in them.

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[51] See Molisch, H., Das Phycocyan, ein crystallisirbarer Eiweisskörper. *Bot. Zeitung,* 53, 1895. Hass, P., and Hill, T. G., *An Introduction to the Chemistry of Plant Products.* London, 1913. Czapek, F., *Biochemie der Pflanzen.* 2te Aufl. 3 Bde, 1913–21.

In the brown algæ, which, for the most part, are inhabitants of the narrow strip of seashore between the tide marks, we have plants occupying one habitat with remarkably uniform environment and alternately with this an environment far from uniform in conditions; for the sea is recognized as exercising such a moderating effect as to reduce changes of temperature and light to a minimum, whereas the air responds to every influence. While immersed in the ocean it is rarely that seaweeds sunburn, though this may happen on bright windless days in the case of matted seaweeds floating just under the surface, as do the great beds of the Giant Kelp (*Macrocystis*) off the shores of the Pacific Coast of this continent. Furthermore, the brown algæ flourish on fog-bathed coasts. At times of fog at least there is no excess of light. It is difficult, therefore, to understand the function of a pigment or pigments in plants living in such contrasting, not to say contradictory, environments. The pigments appear, on microscopic examination of these plants, to be confined in the chromatophores. As extraction by water is slow, there is ample time for decomposition products to form from the system of pigments existing in the chromatophores of live and unhurt cells. We may well believe, therefore, that the contradictory information, which is all that is at present available,[52] is far from giving us an adequate idea of the composition and functions of this pigment, once called phycophæin.

Phycoerythrin,[53] on the other hand, is probably much more like, if it is not identical with, the red protein-like pigment extracted by grinding the red seaweeds (*Rhodophyceæ*) in water in a mortar. In concentrated aqueous solution it fluoresces, and it may be made to crystallize out, characteristic in form and color as hexagonal red crystals. It forms in algæ most of which live constantly submerged in the ocean in an environment of very uniform conditions and with less light than reaches the plants of the land. From this last consideration the inference is easy that the pigments masking the chlorophyll in the red algæ absorb rays of light supplementing those absorbed by the chlorophyll pigments, and also used in the manufacture of food. But experimental or other proof of this is lacking.

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[52] Molisch, H., Ueber den braunen Farbstoff der Phæophyceen und Diatomeen. *Bot. Zeitung*, 63, 1905. Tswett, M., Zur kenntniss der Phæophyceenfarbstoffe. *Ber. d. d. Bot. Ges.*, 24, 1906.

[53] Hansen, E. K., Observations on phycoerythrin, the red pigment of deep-water algæ. *New Phytologist*, 8, 1909.

The red coloring matter of many young leaves in spring, as referred to on page 60, appears to be a very common pigment, anthocyanin.[54] Here again it must be admitted that more than one pigment may be concerned, even if the extracts contain the pigments unchanged from what they were in the living cells. Anthocyanin, or anthocyanins, exist in flowers, fruits, leaves, and stems, all of which are exposed to light, but they also exist abundantly in the roots of the table beet and elsewhere in darkness. Furthermore, their color is red or blue according as the cell sap is acid or alkaline, and correspondingly of the shades between. Owing to their wide distribution, chemical reaction, and diverse duration, the ecologist finds it hard to assign any single function to these pigments, and the physiologist may well entertain the idea in this connection, as in many others, that substances are formed or things are done just because they can be, not because they are indispensable or of any especial advantage. Indeed, even the speculative naturalist should accept such a hypothesis, for in this way may well arise those substances or processes the development of which may lead to that natural selection resulting in disappearance or survival.

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[54] West, C. J., Plant Pigments; the Chemistry of Plant Pigments other than Chlorophyll. *Biochem. Bull.*, 4, 1915.

If we knew the conditions bringing about the formation of the pigments discussed above, we might better understand their uses. The chlorophyll pigments apparently require, in most plants, a certain amount of light, and in all plants a minimum degree of warmth and a minimum amount of iron for their formation. The possible significance of the relation to iron has been previously suggested (see page 69) and will be referred to again (page 125). In evergreen conifers germination may take place, and continue for some time, in the dark, and the cotyledons of the seedlings will nevertheless be green. To this long standing rule I am confident exceptions will be found, if they have not been already, and would suggest that the seedlings of desert and other very well-lighted pines may be found to behave in fashion more like those of the Angiosperms. It is common observation that seedlings and parts of angiospermous plants sprouting and growing in darkness are blanched, are white or yellow or at least not green, and that, other things being equal, they will rapidly turn green when lighted. Since the chlorophyll pigments would be useless in darkness, there is obvious economy in the plants not making them in the dark. On the other hand, light cannot be regarded as indispensable, as furnishing the requisite energy, for example, for the formation of the chlorophyll pigments, or as being the stimulus required to start the protoplasm to form them, since they form in darkness in the seedlings of Gymnosperms.

If the hypothesis of B. Moore, previously discussed (page 70), be correct, the energy absorbed by the chlorophyll pigments is needed for removing the poisonous product of photosynthesis, formaldehyde, made by colloidal iron in the stroma of the chromatophores. If polymerized, it would become innocuous. Energy for the purpose must be absorbed, but it is as difficult to conceive how these complicated pigments are formed in cells coming from darkness into light as to imagine how they came into existence originally. In fact, there is much more ease and comfort in belief in creation than in evolution!

The amount and quality of light requisite for greening has been the subject of considerable experimental study, but none of recent date,[55] so far as I know. In its present state the matter should not be considered settled, and, at times at least, it may be a matter of practical importance to nurserymen who wish to hold back stock for later shipment.

As to warmth as a condition for chlorophyll formation we must, in the first place, recognize that there are minimal temperatures for different vital processes just as there are for physical and chemical processes taking place outside the organism. As fractional distillation is made possible by different boiling points, — *e.g.* of gasoline and other hydrocarbons, of the alcohols, and water, etc. — so we can conceive a temperature at or above the minimum for growth in a given species of plants, but below the minimum temperature for chlorophyll formation. Examples of this are probably more common in mild climates than in severe ones, contrary to first impression, for cool weather persists for a much longer time in California, for example, than is possible in the autumn and spring of the east, separated as they are by the severe winter. Almost every California winter shows bur-clovers (*Medicago denticulata*) and many other plants growing slowly but having their leaves more or less blanched, not by reason of bacterial or other infection, but because the plant lacks the vigor to form chlorophyll, or the chlorophyll will not form itself, at the prevailing temperatures.[56] This is seen often on an extensive scale in grain-fields or grass plots, the blades not blanching but being yellowish until warmer weather makes complete chlorophyll formation possible. Presumably carotin, perhaps xanthophyll, can be formed at lower temperatures than chlorophyll *a* and *b*. This condition, however, should be carefully distinguished from the one previously described (page 60), in which the already formed chlorophyll pigments in the leaves of arbor vitæ, etc., temporarily break down in cold weather and are reconstructed later.

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[55] Wiesner, J., *Die Entstehung des Chlorophylls in der Pflanze.* Wien, 1877. Reinke, J., *Die Abhängigkeit des Ergrünens von der Wellenlänge des Lichtes.* Sitzsb. d. Akad. d. Wiss., Berlin, 1893. Schmidt, A., Die Abhängigkeit der Chlorophyllbildung von der Wellenlänge des Lichtes. *Beiträge z. Biologie d. Pflanzen,* 12, 1913–14.

The condition of chlorosis, — a paling, yellowing, or mottling of the leaves — which has attracted wide-spread interest and been the occasion of much anxiety and investigation, would indicate that, in addition, other factors than iron, light, and warmth are indispensible to chlorophyll formation. While admitting this, it should be remarked that these three factors are more or less specific, at least in degree, whereas the other conditions are indispensable to health which, alone, makes normal existence possible. Without food materials in due proportions, water, oxygen, etc., without proper mechanical support in the soil or otherwise, without all of the other factors of the environment which are the conditions of existence, a plant will not only not form chlorophyll but it will not thrive in other ways, and may not survive. So chlorosis should be conceived not as a specific disturbance of the chlorophyll apparatus alone but rather as a symptom of malaise or ill-health. As such the cause is to be sought, in cultivated plants, in faults of tillage, fertilizing, and irrigation: and one may expect to find that the same appearance is due in different places to different causes, according to the specific circumstances of each case. Because of the large sums invested, for example in orange groves, the impairment of food manufacture by the chlorotic condition of the foliage is regarded with apprehension, and the desire for remedy is correspondingly strong. Hence we find a considerable literature already developed.[57] See also pages 120–132.

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[56] Peirce, G. J., *Studies on the Coast Redwood.* Cal. Acad. Sci. and Contrib. Hopkins Seaside Lab., 1901.

It has long been the legitimate desire of plant physiologists and others to measure the quantities of food made in green leaves, and elsewhere, by photosynthesis. No method so far devised of chemically or physically determining the quantity of starch or sugar or other "photosynthate" has proved itself to be satisfactory. We know, for example, the value of the wheat crop and we know the tonnage or other measure of the crop, but though we may finally realize that its essential ingredients are all made in the chlorophyll-containing cells of the blades of the leaves of the young wheat plants in a single growing season, we do not know the product per cell, per hour, or in proportion to light intensity. We know that the long days of the northern summer offer such compensation for the short season that the great plains of Canada constitute one of the great sources of the world's wheat supply. But we know nothing of the daily quantities out of which these great sums are made. The classical iodine method of Sachs,[58] now ingeniously modified by Molisch[59] for production of photographic effects in leaves, consists, as is well known, in indicating the quantities of starch in a given organ or tissue by utilizing the staining power of iodine, the greater the amount of starch, other things being equal, the darker the characteristic color produced by the iodine solution.

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[57] Kelley, W. P., and Cummins, A. B., Composition of Normal and Mottled Citrus Leaves. *Jour. Agr. Res.*, 20; 161–192, 1920. Gile, P. L., and Carrero, J. O., The Cause of Lime-induced Chlorosis and the Availability of Iron in the Soil. *Jour. Agr. Res.*, 2–: 33–62, 1920 (bibliogr.). Immobility of Iron in the Plant. *Jour. Agr. Res.*, 7: 83–87, 1916. Boresch, K., Zur Frage der Ersetzbarkeit des Eisens bei der Chlorose. *Ber. d. d. Bot. Gesellschaft*, 42, 1924.

[58] Sachs, J. von, *Ein Beitrag zur Kenntniss der Ernährungsthätigkeit der Blätter. I. Die Iodprobe.* Arb. d. botan. Inst in Würzburg, Bd. III, 1884, or Gesam. Abhandl., Bd. 1, p. 355.

[59] Molisch, H., *Pflanzenphysiologie als Theorie der Gärtnerei.* 4te Aufl., 1921.

At the same time that Sachs's method furnishes a basis for comparisons, it obviously does not indicate the quantities of starch in one or another part. To meet this difficulty Ganong[60] describes a method which has been very widely adopted, but without the precautionary reflections which the author's learning dictated. This consists in comparing the weights of discs cut by a sharp cork-borer or punch from the tissue or organ under examination. Conceding that comparable discs may be cut with sufficient skill by such a crude implement as even a sharp cork-borer or punch, if the material is homogeneous or at least uniform, it is obvious to any one at all familiar with the appearance and anatomy of leaves that they are far from being either homogeneous or uniform. The distribution, structure, size, and composition of the veins or nerves (vascular bundles and supporting skeletal parts) are so far from exactly uniform as to outweigh any differences there may be in the size and number even of such solid, though minute, objects as grains of starch. Similarly, comparisons based on the chemical determination of the starch and sugar in equal areas of leaves is also inexact, and may be misleading because of the differences in the structure and composition of the parts, although, if the determinations are made with sufficient skill, the actual quantities in the different parts may be correct.

The methods of Osterhout, and his associates,[61] while admittedly ingenious and moderately satisfactory for the aquatics to which alone they are applicable, give little or no help to the curious student of food manufacture in land plants. The fact remains that energy of low potential — light rays of certain wave-lengths — absorbed by the chlorophyll pigments, mainly in leaves, and applied to two exceedingly stable simple compounds, one of which, carbon dioxide, is present in great dilution in the air, and the other of which, water, is universally present in living bodies, combines these two during the hours of daylight into sugar. The work is done daily, without commotion, with the utmost smoothness and uniformity, and with products of the utmost value, both of which are indispensable. But we can neither readily measure the daily products nor imitate the operation.

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[60] Ganong, W. F., *A Laboratory Course in Plant Physiology*. 2nd ed., New York, 1908, or a 3rd ed. later.

[61] Osterhout, W. J. V., Apparatus for the Study of Respiration and Photosynthesis. *Botanical Gazette*, 68, 1919.

In this connection two additional factors in food manufacture should be considered because of man's occasional interference with the process on which his existence depends. These are full sunlight and pure air.

The classical experiment of Sachs,[62] repeated in every botanical laboratory, shows that the parts of a leaf covered by tinfoil, or other opaque screen, make less food than those parts unshaded, that food manufacture is proportional to illumination, other things being equal, more food being made in bright sunlight than in dim, and none at all in darkness. Man for special reasons may screen his plantations to secure more delicate foliage, as for example in tobacco culture, but by inadvertence he may coat the foliage by the roadside with a more or less opaque layer of dust, or the dust from cement manufacturing plants may accumulate on neighboring foliage, setting in dew or fog as a persistent crust, which even rain cannot remove, darkening the cells beneath more and more as it accumulates and thickens.

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[62] Peirce, G. J., An Effect of Cement Dust on Orange Trees. *The Plant World,* 13, 1910.

In the orange-growing district of the San Bernardino Valley, in southern California, complaint was made over a considerable area against cement dust allowed to escape from the mills. As orange, lemon, and grape-fruit trees are evergreen, their leaves staying on for some years, the accumulation of cement or other dust may become considerable. This was actually the case some years ago, for at that time the dark green glistening foliage of the orange trees was covered by a dull gray coat, through which light neither penetrated inward nor shone through by reflection from within. It was shown in the course of the trial, which established precedents in this kind of litigation, that, by removing the opaque crust from one half of a leaf, thus admitting full light to part of the leaf but making no further change in position or otherwise, four or five times as many starch grains were formed in the cleaned as in the still encrusted parts. This conclusion was reached by counting grains in corresponding cells in the two halves. Sachs's macroscopic iodine-test [63] gave qualitative results of the same sort. The method of cutting out and weighing corresponding discs, as advocated by Ganong [64] and many others, as previously described, is obviously too rough. One is more certain of learning the truth through counting grains that can be seen than by weighing masses of unseen and unknown composition and content. But, it goes without saying that even this simple method must be followed with neatness, skill, and dispatch, pains being taken to prevent or forestall such changes in cell contents as would inevitably take place between the time of collection and examination of the material unless it is immediately killed and is subsequently properly preserved.

The theoretical considerations thus described were confirmed on an extensive and commercial scale by the subsequent experience of both millmen and orange growers; for the former are now retaining, to their great advantage, nearly all of the dust formerly escaping, and the latter are producing oranges and other citrus fruits in normal amount in groves of customary cleanness and beauty.[65]

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[63] Sachs, J. von, *loc. cit.*

[64] Ganong, W. F., *loc. cit.*

The solid atmospheric pollutions mentioned above, and which can be readily removed by various mechanical methods of filtration and precipitation,[66] are more obvious and less dangerous than gaseous ones, naturally quite invisible, and recognizable, if at all, only by the sense of smell or "taste." The usual sources of such pollutions are manufacturing and domestic processes involving the discharge of noxious gases or vapors into the air. Of the fuels in common use by man, wood gives the least offensive smoke, and while this is irritating to the mucous membrane of eyes, nose, and throat, it is not seriously injurious to plants. Thus we may see the wood-smoke from a farmhouse chimney floating upward through the branches of a tree, apparently doing no harm to foliage or branches. But if the farmer resort to coal or even oil as fuel, his tree will quickly record the change by the appearance of its foliage and in time by the death of branches or even the whole tree. The ingredient of the common fuels which is most poisonous to plants is sulphur, which is converted by burning into SO_2, the very irritating gas liberated on igniting sulphur matches. Sulphur dioxide has a marked affinity for chlorophyll. Of Willstätter's four chlorophyll components, chlorophyll *a* and *b* are much more sensitive than carotin and xanthophyll. Hence SO_2 first unites with chlorophyll *a* and *b*, colorless substances resulting, and the yellow pigments becoming recognizable; but if present in sufficient concentration, more or less complete blanching, with the death of the leaf, follows. If, for example, one compare the shade of green of the same species of plants in city parks and in the open country, one will find, in addition to the disfigurement of soot, that the green of the parks is yellower than that of the country. Effects of illuminating gas, to be discussed later (page 287), must not be confused with this. In the air of every coal-consuming city there are, therefore, greater or smaller amounts of SO_2, the presence of which is indicated, perhaps as strikingly as by anything else, by the dilapidated appearance of the firs and other coniferous trees, if any at all survive, and the more or less complete absence of lichens. From a few (two or three) to many parts of SO_2 per million parts of air are invariably present in city and suburban air, with consequences now little heeded.

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[65] See reports of this and subsequent trials in the Superior Courts of San Bernardino and Riverside Counties, California, in Pomeroy's *Reports of Cases Determined in the Supreme Court of California*, 161, pp. 239 *et seq.* San Francisco, 1912.

[66] Cottrell, F. G., Problems in Smoke, Fume, and Dust Abatement. *Ann. Report, Smithsonian Institution*, Washington, 1913.

Illuminating gas more frequently poisons the soil than the air, but some of its effects are more striking than those of SO_2 liberated by burning the coals in general use. Street trees, as distinguished from park trees, are common sufferers from illuminating gas because, nowadays, parks are generally electric rather than gas lighted, whereas gas mains for supplying buildings still lie under the streets. The effect on the soil is indicated to anyone passing by or over a ditch freshly dug down to the gas mains, by the peculiarly fetid odor. Street trees, therefore, rooted in soil contaminated by leakage from gas pipes, suffer accordingly. Even where no other evidence appears, the early and continued dropping of leaves throughout the season is a familiar result of such poisoning. Occasionally one may see a gap in a hedge or even a line in a lawn marking the course of the house-service gas-main.[67] Plants seldom thrive in houses or laboratories. Besides the excessive dryness of the air which only too generally prevails in artificially heated rooms, and the effect of which will be considered later (page 335), house plants which used to thrive especially in the often steamy kitchens and laundries of the last generation or earlier, present a discouraged and far from animated appearance on account of the sulphurous pollution of the air of our furnace-heated houses, still further poisoned by the leaking joints and cocks of gas apparatus. All one need do to confirm this conviction is to bring into the house a number of thriving potted plants from a nursery, garden, or greenhouse, at the same time noticing the odors assailing the nostrils as one enters and passes through the house. If the plants be set in well-lighted spots in different rooms, it will be found that those first show signs of suffering which are in rooms where there are gas appliances, and that the next to suffer are those which are exposed to leaks from a coal furnace.

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[67] Studies of the effects of illuminating gas made by W. Crocker and

Although illuminating gas, and sulphur dioxide from coal are the most general air pollutions harming plants, the great quantities of SO_2 formerly poured out from all smelters in this country treating sulphurous ores, and still given off by the smelters less intelligently operated, produced the most striking examples of great and widespread injury. In certain instances this injury so affected the run-off of the district by stripping the forest cover that communities many miles away from the source of trouble were also affected by flood and otherwise. By reason of the magnitude of the investments involved, — the great smelting corporations on the one hand, the lumber, farming, and stock interests on the other, together

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his associates will be found in the *Botanical Gazette*, 46, 1908, and by T. H. Goodspeed, J. M. McGee, and R. W. Hodgson; Note on the effects of illuminating gas and its constituents in causing abscission of flowers in Nicotiana and Citrus, *Univ. Calif. Publ. Bot.*, 5, 1918.

with the vital but restrained interest of the United States Forest Service — the subject of the effects of smelter smoke upon vegetation and domesticated animals has been examined with extreme care, both in this country and abroad. Owing to the restrictions imposed by the nature of the work, those American botanists engaged in such investigations for some years have published very little. The investigations of their European predecessors, both English and Continental, were released for publication, some of them many years ago;[68] but owing to changed methods and the different scale of operations in this country and abroad, their conclusions were not always applicable to our problems. Hence a very considerable body of information, some of it new and much of it important, has been accumulated without becoming common property. Some of this is to be found in print,[69] much of it, however, is locked in the records of Federal or other Courts, where it is freely accessible but from which it cannot otherwise readily be obtained. The judgments in two of the most important suits of this character are in print,[70] but the evidence is only very incompletely referred to in the decisions based upon it. The experimental work, called forth by the proper desire of scientific men to determine whether what was observed in the field was merely widespread coincidence or was the inevitable effect of a specific cause, has been very extensive; ingenuity has greatly improved the methods; but these are not fully described in print. It may suffice here to state that as a result of these and other experiments, not only was the damage to vegetation by smelter wastes proved, but methods have been devised which utilize the wastes and so prevent the injury, thus profiting both industry and agriculture.

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[68] Consult, for example, Haselhoff und Lindau, *Die Beschädigung der Vegetation durch Rauch*, Leipzig, 1903, and the literature there cited.

[69] Holmes, J. A., Franklin, E. C., and Gould, R. A., Report of the Selby Smelter Commission, *Dept. Interior, Bureau of Mines, Bull. 98*, Washington, 1915. Important bibliography on p. 503, *et seq.*

[70] Johnson, L., The History and Legal Phases of the Smoke Problem. *Trans. Amer. Inst. Mining Engineers*, October, 1917. American Smelting and Refining Co. et al. vs. James Godfrey et al. in vols. 1 and 2, U. S. Circuit Court of Appeals, 8th District, and the *Federal Reporter*, pp. 225–41, vol. 158, 1908. Anderson et al. vs. American Smelting and Refining Co. and United States Smelting, Refining and Mining Co., in U. S. District Court, Salt Lake City, Utah. *Federal Reporter*, pp. 928–44, vol. 265, 1920.

IV

NUTRITION: FOOD MANUFACTURE

Nitrogen

If, as the foregoing shows, little is known as to the manner in which plants actually combine the atomic ingredients of carbon dioxide and water into sugar, thus forming food, it must be regretfully admitted that even less is known about the manipulation of nitrogen. As in the case of carbon, the sources of nitrogen and many, if not most, of the end products, are known; but the means by which the food materials are worked into foods, and the course followed, the reactions taking place, remain for future students to discover. The value of such knowledge to us, and to all other organisms incapable of making their own food, is so obvious that only the extreme difficulty of these fundamental physiological questions offers plausible excuse for our ignorance.

The distribution of carbon is much more uniform throughout the body of the plant than that of nitrogen. Carbon, being a constituent of cell-walls, is contained in all the skeletal parts of the plant, even long after these cell-walls have ceased to enclose any living protoplasm. On the other hand, nitrogen is practically confined to those parts containing living cells. Within the protoplasm, either as one of its constituents, or in one or more of its products, nitrogen exists in the plant. Throughout the body of an animal, even of what may be called, for the sake of comparison, a perennial animal, nitrogen is distributed with fair uniformity. In the body of a perennial plant nitrogen is found almost exclusively in and very near the parts which are capable of growth. Its distribution is, therefore, very far from uniform, though perfectly regular under this rule, as shown by numberless analyses. While approximately one half of the dry weight of the plant body is carbon, the proportion of nitrogen varies from one tenth downward, being greatest in those plants or parts containing least dead tissue. The distribution of nitrogen in those plants or plant parts used as food by man and the herbivorous animals is a matter of great importance, for nitrogen hunger is not necessarily satisfied by those foods containing sufficient quantities of carbohydrates and fats. Potatoes, for example, though containing a large proportion of living cells, have only 1.43–2.81%[1] nitrogenous material in the fresh state and are not a sufficient food for man, while beans, peas, corn, the grains, and spinach, are much more nearly adequate.

The direct source of nitrogen for most green plants is the nitrates of the soil.[2] Since these are freely soluble in water and are found in all natural waters, fresh and salt, in amounts sufficient for the nutrition of the green algæ and other plants living therein, it follows that, wherever there is rain- or snow-fall, the soil will be drained of part of its nitrate constituents. In cultivated soils, therefore, where the soil is washed by rain or by irrigation, and the successive crops remove their due proportions of nitrates, attention must be given to the continuance of an adequate supply of available nitrogen. Nitrogen-containing fertilizer, while not needed perhaps in rich virgin soil, will sooner or later be required. Experience early acquainted man with this necessity, which only later scientific knowledge explained. Thus began the practice, and afterwards the theory, of fertilizers and tillage, which are of the utmost importance in agriculture.

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[1] Leach, A. E., and Winton, A. L., *Food Inspection and Analysis*, 4th ed. New York, 1920.

[2] In 1924 Lipman and Taylor (*Journal of the Franklin Institute*) announced the conclusion, from extensive water cultures of wheat and barley, and from briefer experience with other plants, that these plants at least, and presumably many if not all others, are able to fix the free nitrogen of the air, thus increasing their nitrogen supply correspondingly. Such a conclusion is as natural as one's surprise that nearly all other reports, as well as the "orthodox doctrine" for half a century, are positively to the contrary. In view of the proved reliability of their predecessors and of the recognized ability of these two students of plant nutrition, one must wait for solution of this contradiction, meantime bearing in mind the necessity of conducting experiments on living plants, as well as on human or other animals, under the best possible conditions of purity of atmosphere (not in laboratory air!), suitable humidity, illumination, and temperature, etc.

In uncultivated soil, also, impoverishment will occur unless there are means of maintaining the supply of nitrates. These means are various and include, in addition to (1) the slow weathering of the rocks from which the bulk of the soil constituents come, and (2) the adsorption of ammonia formed in small quantities by electrical discharge in the air and washed down into the soil, (3) the fixation of free nitrogen from the air by certain soil bacteria, (4) the fixation of free atmospheric nitrogen by certain bacteria parasitic in the roots of leguminous and other plants, and (5) the conversion into nitrates by soil bacteria of the ammonia compounds liberated by putrefactive bacteria working in plant and animal wastes. The first of these processes is slow and readily intelligible without description here. The second is of relatively little importance, especially in parts of the world where "thunder storms" are infrequent (for example the major part of California). The third is a factor of safety in the economy of nature, probably insuring the return to the soil of at least as much nitrogen as is lost into the air in the various processes of decay in which uncombined nitrogen may be liberated (see pages 92 ff.). The fourth is a process of great importance in nature and in agriculture, and will be considered later (see pages 98 ff.). The fifth is the most important of all and must be examined in some detail.[3]

If it were not for the activity of putrefactive bacteria the wastes of animals and the dead bodies of plants and animals would cumber the earth, clog the streams, and fill the seas. These putrefactive bacteria break down the organic nitrogenous compounds of these lifeless materials. The free end-products of their activity are ammonia, carbon dioxide, and water. It is seldom, however, that one is able to recognize ammonia, in spite of its characteristic odor, in or over the soil, though one used to be familiar, before the displacement of the horse by the automobile, with the fact that ammonia was generated in quantity from manure and accumulates in imperfectly ventilated stables. The disappearance of ammonia, not sufficiently accounted for by diffusion into the air, may be explained on the hypothesis that, first, it is absorbed as such or as ammonium salts by green plants, or second, it or its salts are acted upon by soil bacteria.

As to the former hypothesis experiment has shown[4] that most green plants in ordinary soils do not find in ammonia or ammonium salts their best source of nitrogen. That the effect of ammonium salts should vary with the kind of soil is not surprising, and the work of Nagaoka and others[5] seems to indicate that rice, to mention a plant of increasing value to Anglo-Saxons, makes at least as good use of ammonium salts as of nitrates.

[3] For a monographic treatment of this subject and an ample bibliography see E. J. Russell, *Soil Conditions and Plant Growth*, 4th ed., London, 1921; and E. W. Hilgard, *Soils: Their Formation, Properties, Composition, and Relations to Plant Growth in Humid and Arid Regions*, New York, 1906.

[4] Hillgard, E. W., *loc. cit.*

[5] Nagaoka, M., On the Behaviour of Rice Plants to Nitrates and Ammonium. *Bull. Coll. Agric.*, Tokyo, 6, 1904, as quoted by Copeland, E. B., *Rice*, pp. 21 *et seq.*, 1924.

As to the second hypothesis we are much better informed, though still lacking knowledge of many details. Ammonia is absorbed in different amounts by various soils, both dry and wet, and especially in the latter combines with certain soil ingredients. Free ammonia, both in the air and in the soil, is injurious to plants except in great dilution; but ordinarily there is no free ammonia in soils upon or in which organic remains are being decomposed, for such ammonia as is not absorbed as above indicated is acted upon, as shown by the remarkable researches of Winogradsky[6] and Omelianski,[7] by soil bacteria. Ordinarily the ammonia formed in the putrefaction of proteins becomes converted, in the soil and in water, into ammonium carbonate. This is acted upon by bacteria belonging, in Europe and Asia, to the genus *Nitrosomonas,* and in America, to the allied genus *Nitrosococcus.* The individuals of the three or more species which Winogradsky describes act upon the ammonium carbonate, forming nitrite, which then is acted upon by bacteria of the genus *Nitrobacter* forming nitrate. These successive oxidations take place according to the following formula in the presence of air (oxygen) in the soil, thus:

$$2NH_4OH + 3O_2 \rightarrow 2HNO_2 + 4H_2O \rightarrow 2HNO_2 + O_2 = 2HNO_3$$

Obviously the acids, uniting with soil ingredients, become salts which are not only harmless but useful. The chemical changes indicated as successive by the formula are practically simultaneous. As previously indicated, there is no accumulation of free ammonia, this becoming carbonate as it is formed by the putrefactive activities of those species of bacteria which attack the remains of plants and animals or which subsist upon the products of those which do. Just as *Nitrobacter* lives upon the product of *Nitrosomonas* or *Nitrosococcus,* and cannot live without it, so we must conceive, as will be more fully outlined later (pages 184–222 under Respiration), of there being an endless chain of organisms living upon each others' products, beginning with the animal or plant, ending with the nitrite- and nitrate-forming nitrobacteria, and including those saprophytic bacteria and fungi which oxidize and metamorphose the otherwise useless remains of larger organisms.

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[6] Winogradsky, S., Recherches sur les organismes de la nitrification. *Ann. de l'Inst. Pasteur,* Paris, 4, 5, 1890–91.

[7] Omelianski, W., Ueber die Nitrification des organischen Stickstoffs. *Centralbl. Bakt. Parasit.,* Abth. II, 1899.

The researches of Winogradsky have shown, further, that the nitrobacteria are themselves incapable of using, and therefore of breaking down, complex plant and animal products, though they subsist upon the ammonia and nitrite made from them by other bacteria. They must have carbon, like any other carbon-containing organisms, for the reasons previously indicated. They obtain carbon, however, neither from organic remains nor, according to Godlewski[8] and Beijerinck[9] from soil carbonates, but from the carbon dioxide of the soil atmosphere. Their source of energy for the synthesis of carbon compounds must be the oxidations which they carry on of those oxidizable nitrogen compounds above mentioned. The nitrites and nitrates, therefore, which they form are by-products, useless to the organisms forming them but immensely valuable to other plants.

As to the fixation in the soil of the free nitrogen of the air, thereby restoring what may have been lost from the soil into the air by the metabolic and other processes taking place in the soil, little can be added to the brilliant results announced by Winogradsky[10] thirty years ago, supplemented by Beijerinck's[11] twenty-five years ago. Winogradsky added a little ordinary soil to a solution containing less than 5% of sugar and very small proportions of common mineral salts but no nitrates. In this solution he found that the sugar was fermented and that nitrogen was absorbed and fixed from the air. The organism accomplishing this he named *Clostridium pasteurianum*. It is small, spore-forming, and rod-shaped. With it two other rod-shaped organisms are associated. Apparently they do not themselves fix atmospheric nitrogen, but without them *Clostridium* can be cultivated only under anaerobic conditions. Owing to the conditions of Winogradsky's experiment, in which he had killed the non-spore-forming bacteria by heating his soil, he did not obtain three other forms which Beijerinck demonstrated also possess different degrees of nitrogen-fixing power, and which he named *Azotobacter, Granulobacter,* and *Radiobacter,* of which the first is the most active and the last apparently only slightly so. The activity of these organisms in artificial cultures is beyond doubt; but their actual productivity in nature varies, without question, according to soil-temperatures and to the chemical and mechanical condition of the soil, compact soils being less aerated than looser ones, and limey soils offering more favorable conditions than acid ones.[12] The end products of these organisms are imperfectly known, and their metabolism and the successive stages in the synthesis of nitrogenous compounds are quite undiscovered except that the yield of nitrogen seems to be 4–8 milligrams per gram of sugar. This seems costly, and does not encourage the application of sugar-containing fertilizers in order to increase production. The application of nitrate fertilizer to the soil seems, at present, to be more profitable, if more nitrate is required.

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[8] Godlewski, E., quoted by Winogradsky in his Chapter on Nitrification, in *Lafar's Technische Mykologie,* Bd. 3, 165, 1904.

[9] Beijerinck, M. W., Ueber die Bakterien welche sich im Dunkeln mit Kohlensäure als Kohlenstoffquelle ernähren können. *Centralbl. Bakt.,* II, 11, 1904.

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[10] Winogradsky, S., Sur l'assimilation de l'azote gazeux de l'atmosphere par les microbes. *Comptes rendus*, Paris, 1893, 1894.

[11] Beijerinck, M. W., Ueber oligonitrophile Mikroben. *Centralb. Bakt.*, II, 7, 1901.

[12] See Russell, *loc. cit.*

Probably other plants besides these bacteria also fix free nitrogen from the air, adding it by their own decay or otherwise, to the soil or the water in which they live. These plants may live by themselves or in association with others. The latter may be discussed later (pages 98–105), but it has long been suspected that algæ, both blue-green and green, have this capacity. Pure cultures by Wann [13] of several species of small fresh water algæ, members of the *Chlorophyceæ,* have convinced him that seven species are able to "fix nitrogen when grown in pure cultures on mineral nutrient agar media containing either ammonium nitrate or calcium nitrate as a source of nitrogen, and glucose, "the amounts fixed" representing increases in the total nitrogen content of the culture flasks of from 4 to 54 per cent."

We must give another moment's consideration to the soil from which most plants secure their nitrogen supply. The bulk of the soil consists of crystalline, or amorphous but crystallizable, material in masses or particles of varying degrees of fineness. Over the soil particles are films of water. In wet soils these films may be practically continuous. In dry soils they may be separate. In either case the films hold in solution the soluble soil constituents, many of which will form ordinary solutions of electrolytes, but others of which will form only colloidal solutions or suspensions. Hence the soil water from which plants secure their requisite nitrogen and other food materials (K, Ca, Mg, S, P, Fe, see pages 120–132) is not at all a simple solution, but a complex one, from which the required food materials are absorbed only as the result of the application of great force (see pages 33–41).

[13] Wann, F. B., The Fixation of Free Nitrogen by Green Plants. *Amer. Journ. Bot.,* 8, 1921.

Having seen that nitrates in the soil, and in the waters fresh and salt containing soil constituents in solution, form the source of nitrogen for most plants, and having seen (pages 19–41) how these enter the plant, we know little besides except the nitrogenous products of the syntheses carried on in chlorophyll-containing, and probably other, cells. The great variety of nitrogenous carbon compounds obtainable from plants fall into different classes according to their complexity or other characters, but it is not justifiable at the present time to do more than to accept as guesswork, more or less learned, any scheme purporting to indicate the probable course or sequence of the successive syntheses from comparatively simple nitrates, through the amino-acids, to the extremely complex proteins of which the living protoplasm consists.

The scope and character of this book are such that a list and description of the many nitrogenous compounds of carbon in the plant body would be out of place. The rôles, whether constructive or passive, of the great majority being unknown, we cannot describe them. The interested reader will, however, find the compounds enumerated in the appropriate places.[14]

As to the place, even, of manufacture of the complex nitrogen compounds which plants and animals use as foods, building them as component parts of their living protoplasm or putting them to other uses (see pages 178–222), there is no agreement. Since the production of protein, and the compounds preliminary thereto, imply the utilization of energy as well as of carbohydrates and nitrates, it is natural to infer that the nitrogenous syntheses, as well as the carbohydrate ones, are carried on in chlorophyll-containing cells, and in daylight[15]: but experiment having shown that, given a suitable supply of carbohydrate and nitrate, green leaves will increase their protein content in the dark,[16] the inference is also drawn that light is only indirectly necessary, as the source of energy for carbohydrate manufacture. But it must be conceded that much remains to be discovered about this subject.

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[14] Czapek, F., *Biochemie der Pflanzen,* 2te Auflage, Jena, 1921. Hass, P., and Hill, T. G., *An Introduction to the Chemistry of Plant Products.* 2d ed., London and New York, 1917. Molisch, H., *Mikrochemie der Pflanzen.* Jena, 1913. Emich, F., *Lehrbuch der Mikrochemie.* Wiesbaden, 1911. Tunmann, O., *Pflanzenmikrochemie.* Berlin, 1913.

We shall have occasion later to discuss the influence of the food materials upon growth and other functions, dependent upon adequate nutrition (see pages 120 ff. and 338 ff.), but attention may now be called to the fact that the behavior of plants, as well as animals, is profoundly affected by their diet and that this in turn may be greatly influenced from time to time by the season, the weather, or some single feature of the latter. Thus the relative proportions, in natural or fertilized soils, of nitrates and moisture in the soil, along, no doubt, with attendant atmospheric differences, which obviously affect the production of carbohydrate but may also influence other processes (see pages 116–119), influence the character of the growth and the fruitfulness of short-lived plants.[17] Thus Kraus and Kraybill claim, among the results of their experiments on tomato, etc., that abundance of nitrates, carbohydrates, and water, result in abundant growth and scanty fruit, whereas a more moderate supply of nitrates and water are followed by less vigorous vegetative growth but more abundant fruit. This simply puts into more definite, though still inadequate, terms the cultivator's long established knowledge that soil may be excessively enriched or irrigated, or that the plants may not be proportionally illuminated, and that then there may well be exuberant vegetation with modest crops.

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[15] See Jost, L., Stickstoffassimilation der grünen Pflanzen. *Biol. Centralbl.*, 20, 1900, where the subject is reviewed and the older bibliography is given.

[16] Zaleski, W., Ueber die Rolle des Lichtes bei der Eiweissbildung in den Pflanzen. *Ber. d. Bot. Gesellsch.*, 27, 1909. Suzuki, W., Ueber die Assimilation der Nitrate in Dunkelheit durch Phanerogamen. *Bot. Centralb.*, 75, 1898. Muenscher, W. C., Protein Synthesis in Chlorella. *Bot. Gazette*, 75, 1923.

[17] Kraus, E. J., and Kraybill, H. R., Vegetation and Reproduction with special Reference to the Tomato. *Oreg. Agr. Exp. Sta. Bull.*, 149, 1918.

We must now consider the special sources of nitrogen and the special ways in which different plants secure their supplies. The means already referred to (page 90) is the association of certain species or varieties of bacteria with the roots of plants, mainly members of the *Leguminosæ.* These bacteria fix free nitrogen from the air, combining it with sugar or other carbohydrate made by the leguminous plant. Other sources are the following — the bodies of other living organisms, upon or within which organisms live as *parasites* (pages 106–112); the wastes and the dead bodies of animals and plants upon and in which organisms live as *saprophytes* (pages 112–116); those products of the activities of soil saprophytes which, accumulating in the soil, are known as *humus* (pages 113–116); and finally the bodies of those insects and other very small animals which may be caught or trapped by the pitcher plants and other so-called insectivorous or carnivorous plants (pages 116–119).

Root Tubercle Plants

The association between bacteria and the roots of clover, alfalfa (lucern), and similar plants has been extensively studied because of the long known [18] beneficial effects of leguminous crops in alternation with grain and similar plantings. The practice of crop rotation, based on centuries of experience, is not even now adequately explained; for, in addition to the benefit to the soil resulting from lying fallow, there may be, and in the case of leguminous plants there certainly is, a distinct gain consisting in addition to the soil and not the mere removal, by leaching or weathering, of deleterious accumulations. As we shall see presently (page 131), accumulated root excretions may reduce the productiveness of the soil if the same plants are too long cultivated therein. These accumulations can be removed during a term of lying fallow, or they may disappear while another crop not sensitive to them is being grown, but in either case the soil gains no constituent. On the other hand, soil analysis shows that ordinarily a leguminous crop, while it may remove certain amounts of calcium, potassium, and magnesium, of which there may be an abundance, will add to the nitrogen content, of which, for the reasons above given, there is seldom more than barely enough, and often there is a scarcity. The legumes are, therefore, extremely valuable, not only as producing food and fodder, but in preserving or improving the fertility of the soil. In Nature the diversity of herbage tends to maintain the fertility of the soil, whereas farm practice, which consists as far as possible in pure cultures, of wheat, corn, or other single crop in a given field, does not. The practice of pure culture is obviously unnatural, and as such, must be offset in the long run by suitable rotation. The cultivation of grain, sugar-beets, and vegetables in succession is often profitable; but the inclusion of a leguminous crop in the succession is generally more beneficial because of the gain in soil nitrogen under the leguminous crop, whereas the other crops make no such addition. The reason for this gain was revealed by the researches of Hellriegel and Wilfarth,[19] nearly forty years ago, who found that legumes growing in unsterilized soil developed tubercles on their roots but did not do so in sterilized soil, that in unsterilized soils deficient in nitrogen they nevertheless throve, adding to the nitrogen content of the soil, and that these tubercles were the result of bacterial infection.

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[18] Russell, E. J., *loc. cit.*, p. 184, footnote, says that this practice was known to the Romans, as indicated in Book I, line 73 of Vergil's *Georgics.*

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[19] Hellriegel, H., and Wilfarth, H., Untersuchungen über die Stickstoffnahrung der Gramineen und Leguminosen. *Beilageheft d. Zeitschrift d. Vereins f. d. Rübenzucker-Industrie d. deutsch. Reich.*, November, 1888.

Many persons in various countries have published studies of the organisms causing the formation of tubercles on the roots of leguminous plants, the development of the tubercles from infections of the root-hairs, the development (or degeneration) of the organisms themselves, the action of the organisms as fixers of atmospheric nitrogen, the contributions of the leguminous plants to soil fertility and the organs in which nitrogen absorption is accomplished. Beijerinck [20] and Prazmowski [21] appear to have been the first accurately to describe the infecting organisms. *Bacillus radicicola* is the name generally given to the organisms causing root-tubercles to form; but there are convincing reasons to believe that there are many varieties at least, or strains, differing from one another as do strains of yeast or breeds of cows in the rate at which they work, and in the quantity of the products. These bacteria are aerobic rods as shown by pure-culture, but in the tubercles of leguminous roots they increase in size and branch, forming Y or T shaped "bacteroids." They have not been isolated as such from the soil; but that they are present in most soils in vegetative or spore condition is obvious from the fact that leguminous plants develop tubercles on their roots if cultivated on most soils unsterilized, but do not do so if the soil is heated to 75° C. or subjected to the action of antiseptic vapors. The latter method has been resorted to in order to avoid the evils complained of in all methods involving destructive heats; for any temperature high enough to fix bacterial protoplasms will also coagulate some if not all of the proteins and will more or less profoundly affect all the other colloidal contents of the soil. Calcining, which Frank [22] resorted to, not only killed the whole microflora and fauna of the soil, but it also more or less changed or destroyed the lifeless humus and other heat-sensitive soil constituents. On the other hand, chemical antiseptics should not be regarded as being so perfectly selective that they can affect only those living organisms in which we are interested, leaving untouched substances outside the organism which are, nevertheless, the same or similar to those within.

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[20] Beijerinck, M. W., Die Bacterien der Papilionaceen-Knöllchen. *Bot. Zeitung*, 46, 1888.

[21] Prazmowski, A., Die Wurzelknöllchen der Erbse. *Landw. Versuchsstat.*, 37, 1890.

In unsterilized soils seedlings of leguminous plants become infected through their root-hairs. Experiment has shown that, whereas a grass-seedling would escape root infection by cutting off the infected tips of its root hairs by new walls formed below the point of infection, no such division or exclusion walls are formed in the infected hairs of leguminous plants.[23] In the infected root-hair, after the necessary period of incubation, during which the infecting individuals of *Bacillus radicicola* have multiplied into a thread-shaped mass, this thread or strand grows into and through the successive cells further and further from the surface of the root until, having reached that layer (the pericycle) which, when stimulated, forms lateral roots, successively infects the parenchymatous cells of a mass which would ordinarily become a lateral root but which presently aborts, though it may continue to grow, persisting as a tubercle even more deformed than those lateral roots misshapened by the hard conditions of existence in which they must combat physical, chemical, and living agents in order to survive.

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[22] Frank, A. B., Ueber die Pilzsymbiose der Leguminosen. *Landwirthschaftliche Jahrbücher,* 1890.

[23] Peirce, G. J., The Root-tubercles of Bur-Clover (*Medicago denticulata,* Willd.) and of some other Leguminous Plants. *Proc. Cal. Acad. Sci.,* 3d Ser., Botany, 2, 1902.

It is clear that, given the necessary culture medium, these organisms can be kept in pure culture outside the leguminous plant, under such conditions fixing free nitrogen from the air and passing through various forms of development. But though it is known that, if the organisms are supplied with carbohydrate and if their products are drained off with due care, they will fix even considerable quantities of free nitrogen from the air, the means and the course by which they do so, combining it with carbohydrate probably to soluble proteins, is not known.

These cultures, more or less pure, have come into agricultural commerce under various trade names, of which perhaps Nitragin is the best known, different cultures being sold for different crops, in order to increase the productiveness of the soil. In the first place, most soils contain leguminous weeds, examination of the roots of which will instantly disclose whether they have formed tubercles or not. If they have, the presumption is reasonable that the soil contains the organisms requisite for infecting the roots of the proposed crop. Thus alfalfa (lucern) can be sown with confidence in any soil in which bur-clover or other wild clovers grow. The purchase and addition of nitrogen cultures to such soil would, therefore, seem superfluous; and if the addition should, by chance, not be made until after the crop was well started, such infections as took place might do more harm than good to the legumes. It is evident that these latter can profit only if the bacteria have sufficient time in which to accumulate an excess of nitrogenous carbon compound or compounds to be passed on to their host plants in return for the carbohydrate taken. There are also some few leguminous plants apparently immune to such infections, though perhaps none the less important in nature and useful to man.

From the foregoing description it is obvious that the roots of many plants, especially members of the *Leguminosæ,* are liable to infection through their root-hairs, by minute organisms which grow into rod or Y or T shaped bacteria in the parenchymatous tissue of the root of the host, distorting or disfiguring the root by hypertrophies known as tubercles, in which these bacteria absorb and combine the free nitrogen of the air with carbohydrate absorbed from the host. If such combined nitrogen exceed the normal needs of the bacteria themselves, it will be absorbed by the host, thus offsetting the drain of carbohydrate by the bacteria. Until such return in the form of combined nitrogen, the loss of carbohydrate to the bacteria is in no respect different from that in any other association in which the host completely nourishes the parasite; but with this return we begin to have the so-called mutually beneficial association, an association which finds its best, though still very imperfect, development in some of man's associations with his fellows. It is to be noted, however, that whether the leguminous plant ever profits from its infection, the soil gains, at least for a time, and it is in this soil gain, rather than plant or crop gain, that the farmer receives his greatest benefit. Nevertheless, it seems conceivable that, in studies designed to increase crop-production, attention devoted to study of the strains of root tubercle-forming bacteria as to their N-fixing power, carbohydrate consumption, and most productive hosts might yield valuable results.

Furthermore, the practice of summer fallow, a conspicuous feature of the so-called "dry-farming" methods of the semi-arid west, is so unnatural, so wasteful of time and of acreage, that one is justified in seeking ways of profitable escape. Excuse for it is made on the pretext that summer fallow conserves the soil water. Since, in dry farming as distinct from irrigation, it is the rain or snow which falls upon the soil, rather than that which may come laterally and then upward from the deeper layers of the soil, which the plants use, care in the selection of crops so that their water requirements shall not exceed the water capacity of the region should lead to better results than are now obtained. The fertility of these dry farm soils requires no less attention than that of other soils, but the methods to be employed must be as accurately accorded to the conditions as the crops. Indeed, using the fundamental idea of crop rotation, it would seem that the dry farmer who desires to raise wheat, should not only secure and preserve the variety of wheat best suited to his conditions, but he might advantageously seek a drought-resistant short-lived legume to sow in the off years, instead of letting his land lie fallow, a source of expense with no return.

The beans native in desert regions,[24] whether of Arizona or of other parts of the world, furnishing food or feed to man and other animals, should be studied for this purpose. These beans, thriving under minimal supplies of water should yield a merchantable crop, giving thus an additional income. They should, by being mowed and thus leaving the roots in the soil, add to its nitrogen content and its productiveness. As to the amounts, if any, of soil water which they would remove it is obvious that knowledge is at present but imperfect. The advocates of dry farming pronounce that summer fallow under dust mulch conserves the stock of soil water, whereas a crop reduces it. On certain dry farm areas the water in the soil can be only that which falls upon it as rain or snow. There can be no supply from below. Of what falls, a part will be immediately lost by evaporation, another part will be lost to that particular spot by migration vertically and perhaps, at depth, laterally. The remainder will remain for a longer or shorter time in the soil, held there more or less firmly by the soil particles according to the composition and physical condition of the soil, and drawn out of it only by evaporation and transpiration. Evaporation can be materially reduced by mulching, a dust mulch cutting it down to approximately one half of what would occur under the same conditions from a continuous surface to which capillaries lead uninterrupted from below. It is the breaking of the soil capillaries into very short lengths by the plow and the harrow that makes the dust mulch useful. But transpiration will also vary greatly according as mesophytes or xerophytes occupy the soil.[25] Some plants are "great drinkers," others the reverse. Desert herbs thrive on quantities of water quite insufficient for other plants. Let us, therefore, have studies by the botanists of the Experiment Stations, and others, of the desert legumes, with a view to substituting food production for the unnatural, unproductive, unprofitable practice of summer fallow. I am not oblivious of the necessity of cultivating a market as well as a crop; but no one who is old enough to recall the increase in consumption of grape-fruit in this country, or, to cite a much more recent and perhaps even more striking example, the casaba melon, will doubt the feasibility of educating the buying and consuming public.

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[24] Freeman, G. F., Southwestern Beans and Teparies. *Bull.* 68, Agric. Exp. Sta., University of Arizona, 1912.

Thus the plant physiologist, interested in leguminous plants as the symbiotic associates of certain bacteria contributing to soil fertility and productiveness, would like to see their use extended for the benefit of a hungry world.

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[25] See pp. 333–340.

Parasites

Complete parasites, animal and plant, are organisms which obtain all their food from other living organisms. Thus we have animal parasites living in the bodies of other animals (tape-worms for instance) and in the bodies of plants (for example leaf, bark, and other borers); plant parasites living on or in the bodies of animals, as those fungi and bacteria which cause disease (for example, the fungus causing herpes and the bacillus of typhoid), and on or in the bodies of plants (as the various sorts of mistletoe, the fungi causing mildew, rust, and rot, and the bacterial infections). Owing to their great hygienic and economic importance parasites of all kinds have received much attention; but it is to be regretted, even for "practical" reasons, that investigations have progressed so little beyond the descriptive stage. The life histories of the tape-worm, the bacillus of typhoid, and the rust of wheat, for example, have been worked out; but, beyond the general principles, little is known of the actual chemical processes and products involved in their activities and their effects. The theory of toxins and antitoxins, and susceptibility and immunity, while based on a certain amount of very valuable experience and knowledge, remains a theory for lack of definite knowledge of the toxins and antitoxins themselves. The physiologist engaged in studies of parasites and parasitism finds expert knowledge and operative skill as a chemist quite indispensible; but the chemist who lacks physiological knowledge and experience finds himself working on dead matters and on the products of living organisms when he might wish to study the organisms themselves. For the reasons thus suggested or implied, knowledge of parasitism, whether the cause of disease and death or only of deformity and discomfort, is grievously deficient.

By this frank acknowledgment of deficiency the desirable subjects of investigation are also indicated to the student, whether he be attracted by pure or by applied science. The hygiene and well-being of the forest, the field, the farm, and the family involve a knowledge of parasites and parasitism; and the evolutionist finds ample temptation to speculate as to the origin and development of parasitism in the various degrees of parasitism to be observed.

Parasites differ from other organisms only in the varying degrees of their dependence upon other organisms for foods. It may appear that certain of the European and American mistletoes, *Viscum* and *Phoradendron,* are able, if supplied with water and other raw materials by their hosts, to manufacture sugar and other foods for themselves; [26] but this is not true of them all. *Phoradendron juniperinum,* of the Sierra Nevada Mountains in Central California, resembles the species of *Arceuthobium* (*Razoumowskia*), *Rafflesia, Brugmansia,* and many parasitic fungi, in vegetating, growing and spreading, completely imbedded as colorless filaments or masses in the tissues of the host, sending out green or olive green branches bearing the pistillate and staminate flowers and ultimately the fruits.

As we have previously seen (pages 47 *et seq.*), organisms devoid of chlorophyll (or its equivalents, if any) cannot make food, they must get it from other organisms. The mistletoe of Europe, *Viscum album,* has been called a water parasite, for it is green and robs its host of water and mineral salts, not of sugar and its derivatives, taking carbon dioxide and oxygen from the air. It, and the California *Phoradendron villosum* appear, however, to kill the terminal portion of the branches on which they grow. Is this brought about by cutting off their water supply or by "intoxication"? We do not know. The structural relations of these parasites and their host have been well worked out,[27] but though the phloems of the two are not directly connected, the inference that there is no absorption of sugar and other food by the mistletoe is not justified. There is no evident reason why there should not be movements of foods in either direction, according to circumstances, but these movements are not likely to be such as to make mistletoe infestation a benefit rather than a bane. In all cases of *Viscum, Phoradendron,* and *Arceuthobium* attack with which I am acquainted there is, in addition to the more or less evident injury to the host, due mainly perhaps to water loss, such a weakening or destruction of the woody tissues as very greatly to weaken the branch or trunk, making its breaking in storm more probable and impairing or destroying its value as lumber.[28] There is no reason to conclude that this injury is purely mechanical. In fact there is decided evidence, in the cases examined by Boyce[29] to conclude that there is physiological injury also resulting from the association. But injury does not constitute parasitism, though it is a common consequence of it.

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[26] See Bonnier, G., Assimilation du Gui comparée a celle du Pommier. *Bull. Soc. Bot. de France,* 1890. Sur l'assimilation des plantes parasites à chlorophyll. *Comptes rendus,* CXIII, 1891.

Although all animals and many plants are completely dependent upon green plants for food, only those are said to be parasitic which are in close bodily association. Except for the colonial organisms among the "lower" plants — the volvocaceous algæ for instance — the only associations properly so-called among plants are those of more or less diverse sorts and of very diverse benefit to the components. There is no co-operation, there is only competition, among individual plants. The vegetable kingdom, in fact, is one of almost complete, almost perfect, individualism. This fact may well furnish ground for much reflection by the philosopher, social and other.

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[27] Cannon, W. A., The Anatomy of Phoradendron villosum. *Bull. Torrey Bot. Club,* 28, 1901.

[28] Meinecke, E. P., Parasitism of Phoradendron juniperinum libocedri Engelm. *Proc. Soc. Amer. Foresters,* 7, 1912.

[29] Boyce, J. S., The Dry-rot of Incense Cedar. U. S. Dept. Agric., *Bull.* 871, Washington, 1920.

Complete dependence for food is shown by the various species of dodder, *Cuscuta,* parasites causing serious losses in the flax and clover fields of Europe and in the alfalfa (lucern) fields of our own country. The injury which the dodder does to flax is presumably mechanical as well as chemical, destroying or at least greatly impairing the flax stalks as a source of linen fiber. The mechanical injury it does to clover and alfalfa or other forage plants may be of minor importance; but there can be no question of the comparative worthlessness of dodder infested alfalfa and clover as hay, even if such fields produce any. We have here, then, an example of the poisoning, intoxication, of a host by a parasite, intoxication in many cases fatal and serious in all. The seriousness of dodder as a pest in food and flax fields is indicated by the values of the possible crops as compared with actual yields when dodder attacks them. There is no possibility of combating dodder by breeding disease resistant strains, as is the admirable practice in dealing with bacterial and fungus parasites. Only exclusion, by quarantine and otherwise, is possible, a method made all the more difficult in the case of alfalfa by the similarity in size and color of the seeds of the host and parasite.

The germination, attack, penetration, and growth of dodder will be discussed later (pages 265–266). Here we need go no further, recognizing that, by robbing its host of sugars, and very likely nitrogenous foods, also, as well as water and mineral salts, dodder impoverishes it; but it probably still further injures it by its own metabolic products which, dialyzing into the host through the haustoria, poison or otherwise hurt it. Such drainage and consequent injury are at once recognizable in the cases of those parasites, fungous, bacterial, algal, and phanerogamic, which are completely enclosed, at least for a time, within the bodies of their hosts. Poisoning or other injury by this means has been called intoxication; and as in the case of diphtheria, typhoid, etc., definite chemical products of parasitic activity have been postulated, though not isolated or otherwise recognized except by their effects, under the name of toxins, and noble efforts have been made to combat them by means of so-called antitoxins, of which von Behring's diphtheria antitoxin is the most widely and gratefully known. So far, the students of plant pathology have only begun to follow the example of their colleagues in animal pathology in devoting themselves to chemical studies designed to determine the effects in order the better to combat disease. Here lies a field of great interest, as well as great practical importance for the chemically equipped physiologist and pathologist, a field in which the results to be attained are as much more definite as the methods are more exact than those of the plant breeders, who hope, by the method of trial and error, to discover strains immune to infection. It may be hoped that the remarkable energy of which the plant pathologists give such striking evidence may be increasingly directed toward studies which will enable us better to understand the exact effects of parasitic infestations, and thus suggest more effective and economical means to prevent them. As it is, the physiology of plant parasitism has made little advance beyond the realization of the varying degrees of dependence of the very large number of parasites, both flowering plants and other, upon their hosts for water and dissolved foods and food materials.

In addition to the parasites previously mentioned (the mistletoes and dodders) there are many species of flowering plants which are more or less completely parasitic, attacking the branches or stems of their hosts above ground or their roots below, vegetating within the tissues of their hosts and emerging only to flower and fruit (*Rafflesia, Brugmansia*) or remaining always outside and drawing their sustenance through modified roots (haustoria) which penetrate and connect with the tissues of their hosts (*Loranthaceæ*). This is not the place for a list of these species. They are only incompletely enumerated in the manuals of plant pathology, because many of them attack plants of no present economic importance. On the other hand, the fungi and bacteria which cause plant disease are described in the books on plant pathology.[30]

Because of the peculiar results, we may speak here of those associations between certain, generally undetermined, species of fungi and unicellular or simple filamentous fresh-water algæ known as lichens. These growths, considered to be individual plants, have been proved to be the product of their very diverse components,[31] the one capable of independent existence wherever water, light, and food materials are available, the other powerless to make any food and dependent upon the products of the photosynthetic and other activities of other organisms. The fungus component of lichens is parasitic upon the alga, perhaps manuring the alga with its by-products, perhaps poisoning as well as exhausting it, perhaps clothing it against heat, cold, and evaporation, but in any case enslaving (domesticating!) it, and producing jointly with it growths peculiar in appearance, distribution, and properties.

Under certain conditions lichens, ordinarily quite innocuous, may so overgrow the plants upon which they are as to injure them. Thus I have seen foliaceous lichens spreading over beds of moss, fruticose and other lichens crowding the twigs of fruit trees, and filamentous ones hanging from forest trees in fog or cloud channels. In such cases the lichens no doubt impede the exchange of carbon dioxide and oxygen, absorb light, "smothering" the substratum and perhaps also acting upon it by its own soluble metabolic products, for rock-covering lichens are known to exert a solvent action upon the rock, beginning or hastening its disintegration into soil.[32] Since lichens appear to be especially sensitive to liquid and gaseous poisons, sprays, fumigations, and volatilizing dusts (sulphur, etc.) may be successfully employed by the horticulturist to rid himself of these pests.

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[30] Stevens, F. L., *The Fungi which Cause Plant Disease.* New York, 1921. [31] De Bary, A., *Die Erscheinung der Symbiose.* Strassburg, 1879.

Saprophytes

The distinction usually made between parasites — organisms living at the cost of other living organisms and in close bodily association with them — and saprophytes — organisms living on the lifeless products of other living organisms — is artificial, designed to secure convenience and to express a truth, but often inconvenient and misleading. Caterpillars, snakes, lions, directly devour the still living tissues of their victims as well as the lifeless contents and products of their cells. One does not think of parasites doing more than consuming the lifeless contents and products of the living cells of their hosts, however close the contact of living host and living parasite may be. Saprophytes also consume the lifeless contents and products of living cells, but they do so without close bodily association with the organism or organisms from which their food comes. Both parasites and saprophytes require other living organisms to prepare their food, but parasites follow food production much more closely in time and in space than do saprophytes. Thus the sources of the organic carbon compounds, nitrogenous and non-nitrogenous, of parasites and saprophytes are the same; but parasites can and often do affect their food producers, whereas saprophytes cannot. In the former case we have association, symbiosis, of diverse organisms. In the former we may have organisms living on the abundance of the products of their hosts, or impoverishing and exhausting them. In the latter we have organisms living on the lifeless remains of other living organisms. The physiological principles of absorption and nutrition are the same as for all other organisms, the lifeless remains and the lifeless wastes of living organisms merely offering the sources of carbon, nitrogen, and other needed elements of food in more or less complex compounds instead of in the simple food materials in air and soil. But some apparently saprophytic plants are found to be only parts of close bodily associations consisting of flowering plants and fungi; and some associations between soil fungi and the roots of independent plants are evidently those between fungi living in part as saprophytes in soils containing substances derived from organic remains or wastes and in part as parasites upon the roots of the green plants. There might seem to be a feasible and valid distinction also between, *first,* those bacteria and fungi which, attacking dead bodies of animals and plants, begin the destructive processes which finally reduce these complicated machines to the raw materials out of which they were formed; and *second,* those bacteria, fungi, and other plants which live in *humus,* the "indefinite and complex mixture"[33] of organic compounds formed in the soil from the wastes and remains of organisms by the activities of the first group. The distinction is not feasible, however, because one link in this chain of destructive processes seems to be missing or to be longer than the rest. These different conditions may be made more intelligible by examples.

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[32] Bachmann, E., Die Beziehungen der Kalkflechten zu ihrem Substrat. *Ber. d. d. Bot. Gesellsch.*, 8, 1880.

[33] Russell, E. J., *Soil Conditions and Plant Growth,* 4th ed., p. 133, 1921.

Mushrooms, toadstools, the white mycelia in leaf mold, and the small, inconspicuous, but extremely important fungi and bacteria of soils containing humus, which is a complex of colloidal and crystalloid products, by-products, and results of animal and plant activities, are saprophytes. They contain no chlorophyll, cannot make food for themselves, must obtain their carbon and nitrogen in already fairly complex compounds. Among these the putrefactive bacteria and their successors break down the complex proteids, carbohydrates, etc., of the animal or plant body, its excreta or remains, to simpler and simpler compounds, which are absorbed by one or another saprophyte and converted into new living protoplasm or put to other use. Thus humus is made and maintained, utilized and destroyed, the residence and the nourishment of unnumbered species of living organisms, which keep the nitrogen cycle intact (see pages 89–91 ff.).

A considerable number of species of flowering plants devoid of chlorophyll live by association, on and in their roots, with soil fungi. The name *mycorhiza* was given a quarter century ago by Frank,[34] to associations between roots and soil fungi. Obviously the flowering plants, of which perhaps the Indian pipe, *Monotropa,* the Snow plant, *Sarcodes,* and Pine Sap, *Hypopytis,* are the most generally known, must obtain already elaborated carbon compounds. Apparently they cannot do so through their own roots directly from the humus in which they live, the fungus filaments or web covering the roots apparently acting as the intermediary, absorbing from the soil and being absorbed from by the larger flowering plant.

Morphologists distinguish between endotrophic mycorhizas, in which fungus filaments penetrate the cells of the " host " by means of haustoria, and exotrophic mycorhizas, in which the fungus filaments simply invest the tissue or organ of the host. Absorption in both cases follows the same physical and physiological laws as in other organisms, but the mycorhiza fungi undoubtedly work over, to the advantage of their dependent hosts, the nutritious ingredients of humus. Under the same physical and physiological laws the fungus component will receive in return such substances as it may use. An association of this sort, therefore, may be said to be mutually beneficial.

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[34] Frank, A. B., *Die Bedeutung der Mycorhiza-Pilze für die gemeine Kiefer,* Forstwissenshaftliches Centralblatt, 16, 1894.

When, however, mycorhizal fungi are associated with green plants, the association may be of a very different nature. Such associations have been described as occurring in many of the *Orchidaceæ, Ericaceæ, Cupuliferæ, Coniferæ,* in certain ferns and liverworts. One naturally suspects that association of a plant which, by making its own sugar and other foods, is quite independent (orthotrophic) with another unable to utilize any but elaborated foods (heterotrophic), is an association of host and parasite, the parasite certainly securing sugars and perhaps other foods from its host, whatever it may contribute in return.

Still another sort of association should be mentioned in this connection. Certain green, and therefore self-feeding and independent, plants are in actual bodily association with other green or blue-green and therefore presumably self-feeding and independent plants, just as there are certain animals in which green algæ live. In the liverwort, *Anthoceros,* there are *Nostoc* filaments, in the water fern, *Azolla, Anabœna* filaments, in the fronds of the diminutive flowering aquatic duck weed, *Lemna,* there are various unicellular green algæ, in the aerial roots of *Cycas* and other plants there are green and blue-green algæ, in the leaves of certain jungle plants algæ have also been described, in *Hydra, Convoluta,*[35] and various other animals, algal cells are regularly found living. In all of these associations we can see possible nitrogen supplies to the algæ. This may be imagined to be especially the case with the algal associates of animals.

It is possible to cultivate the members of these associations separately; but to infer, if either or both should not thus thrive, that the association is beneficial to one or both, or to conclude, if either or both should prosper separately as never together, that the association is harmful to one or both, is demanded neither by the rules of logic nor by general experience. All that separate culture has yet shown is how the quondam associates behave under the methods of cultivation tried. It is more reasonable to see, in such associations, examples of behavior occurring not because it is beneficial but because it is possible. One may, if one is young enough, get over a fence in many different ways, some more amusing, more expeditious, more destructive, more certain, than others; but though it is possible to get over this hypothetical fence, it may not be at all necessary, one may go around or through or not go at all! Apparently many things exist or happen in Nature for no other reason than that they can. Out of three possibilities, time, circumstances, and variation may develop advantage or disadvantage, the material for selection, another step in evolution or degeneration.

Carnivorous Plants

Carnivorous plants have furnished, if not the material, at least the suggestion, for a great amount of botanical fiction, and when scientifically treated they may well be considered as belonging to taxonomists, plant geographers, and ecologists;

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[35] Keeble, F., and Gamble, F. W., The Bionomics of Convoluta Roscoffensis, with Special Reference to its Green Cells. *Quart. Journ. Microsc. Sci.,* 1903, *et seq.*

but the peculiar way in which they are supposed to supplement their nitrogen supply is properly within the scope of physiology to discuss. These plants capture or entrap insects and other small animals, if available. Thus *Dionœa* of the Dismal Swamp in North Carolina, *Drosera* of remarkably wide-spread distribution throughout the cool temperate, and especially the wet and humid, parts of both the northern and southern hemispheres, and *Pinguicula,* living in swamps and bogs, in soils conceivably deficient in nitrates through leaching, are known to capture flies, etc., which may alight on their outstretched and highly irritable leaves: and *Sarracenia, Darlingtonia* and the *Nepenthes,* living in similar position or pendent from trees, digest such creatures as may fall into their pitchers. *Utricularia,* commonly included in such a list, is an insect catcher apparently only when it lives as a submersed aquatic, for the bladders of amphibious plants are small, impotent, and empty.[36]

It is generally conceded, since the classical experimental work of Charles Darwin,[37] that the insect catcher, *Drosera,* and its like, do actually digest the nutritious parts of the bodies of such insects or other small animals as may come upon and be caught by the irritable leaves. This digestion of protein and other complex organic nitrogenous compounds, while it may be accomplished in part by such autolysis of their own tissues as may occur after the insects are caught and die, is done mainly by peptonizing enzyms actually secreted by the glandular hairs or the otherwise glandular surface of the leaves. On the other hand, the insect trappers, with water partly filling their pitchers and exposed to inoculation from the air, continue to be discussed as possibly not digesting their prey but merely absorbing the products of putrefactive bacteria attacking the drowned insects. Hepburn [38] and his collaborators, working on *Nepenthes*, have continued the studies of Macfarlane, and many others, whose work they cite, and conclude that, since the liquid in unopened and therefore unexposed pitchers is sterile, infection takes place from the air and is effected also by the insects themselves as bacterial carriers, and that, in comparison with the activity of the protease secreted by the pitchers themselves into the pitcher liquid, bacterial digestion is slow and ineffectual.

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[36] I wish to take this opportunity to acknowledge the value of a great herbarium and the courtesy of Professor Benjamin Lincoln Robinson, Professor Merrit Lindon Fernald, and the late Miss Day, Librarian, of the Gray Herbarium, Harvard University, in this and many other matters treated in this book. In an hour and a half I looked at many specimens of *Dionœa, Drosera,* and its allies, *Pinguicula,* and *Utricularia,* from the Americas, Australia, Africa, and Europe, scrutinizing them for insect remains. Such a comprehensive view would be possible only in one of the very few *great* herbaria of this country or Europe; the smaller herbaria could not give it. I am very grateful, as a physiologist, for the opportunity. One sometimes hears that systematic botany and herbaria are outgrown and useless. This is as ludicrous as to say that feet and legs are outgrown and useless to the scholar because he is engaged in intellectual pursuits. A more intelligent view of science will lead to grateful acknowledgment of the soundness of a part of its foundation.

[37] Darwin, Charles Robert, *Insectivorous Plants.* New York, 1889.

Actual observation of "wild" plants living under natural conditions in their native habitats, and of herbarium specimens of "wild" plants, show that while some individuals may catch many insects, many individuals catch very few, at the present time. But the very wide distribution, the extraordinary features, and the permanence of the peculiar morphological and physiological characters of these plants, all mark them as the descendants of ancient forms, largely living in the humid tropics, under conditions also favoring an abundant insect life. That their carnivorous habit is now of minor importance is indicated by the following facts. In the *first* place, the uncertainty of this source of food owing to the scarcity or irregularity of insect distribution and the small size and the inconspicuousness of these plants: *second,* the great number and variety of other plants at least equally prosperous, which live side by side with the carnivorous ones but without nitrogenous food from the air: *third,* the continuing supply of nitrogenous foods or food materials for all swamp plants furnished by the humus always abundant in swamps.

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[38] Hepburn, J. S., *Biochemical Studies of Insectivorous Plants.* Contrib. Bot. Lab., Univ. Penn. Philadelphia, 4, 1919.

The value of this last factor seems curiously to have been underestimated. It is obvious that nitrates would be rapidly removed from the wet soils of swamps, going in solution into the pools and streams. On the other hand, the litter of swamp life, animal as well as vegetable, broken down by putrefactive bacteria, forms humus, in which the same supply of nitrogenous foods or food materials would continually form by bacterial and fungus action as we have already seen to be the case in dryer humus (pages 113–115). A careful study of the microflora of these swamp soils, and of the mycorhizal associations possibly existing, should be undertaken by those still curious about these ancient plants.

V

NUTRITION: FOOD MANUFACTURE

Ash Constituents

When plant and animal tissues are burned the carbon, hydrogen, oxygen, and nitrogen escape into the air, as gaseous compounds (and free nitrogen?) leaving the familiar, more or less gray, residue, ashes or ash. This contains, besides many other substances present merely incidentally, because they are in the soil or water in which the plants and animals live, those elements also which are indispensable to all living things. These elements are potassium, calcium, magnesium, sulphur, phosphorus, and iron. Sulphur and phosphorus are constituents of protoplasm, invariably present in the cytoplasm or the nucleus of the cells. Magnesium is an ingredient of one or more chlorophyll pigments, as recently shown (see pages 58 ff.). Potassium, calcium, and iron are not yet known to be constituents of the living material of the plant, although iron is a structural element of the hæmoglobin of the blood and of certain other animal substances.

Experimental cultures in soil, powdered glass, or pure washed quartz sand, and in solutions (water cultures), have proved that, without these ten elements, no plant or animal can live. The majority of these ten are seen, as above, to be constituents of protoplasm or of its indispensable products, certain of the chlorophyll pigments. Attempts to cultivate plants without iron are prosecuted with the utmost difficulty. On the other hand, small amounts seem to be sufficient. Sachs's dictum,[1] that iron is indispensable to chlorophyll formation has been generally accepted as true, in spite of the conviction that iron is not a constituent of any of the chlorophyll pigments. Iron has therefore been generally, but vaguely, conceived to be indispensable only as one of the factors or conditions of chlorophyll-formation, as warmth is, or as light generally is. That the function of iron may be more definite than this has been previously suggested (see pages 68–79), and is indicated, perhaps in still more definite form, by Pollacci and Oddo.[2] Admirable as the intent of these papers is, namely, to lead us to definite knowledge of the work of iron in the plant, time alone can show whether these conceptions are so correct that we can incorporate them into the body of scientific fact. As already indicated, the assertions of chemists working with living things are naturally accepted somewhat slowly, though no less appreciatively in the end, by those working with less violent means among and upon living organisms. In any event, the quantity of iron ordinarily requisite to normal coloration in green plants is so very small that it is likely to be present without special pains being necessary to provide it. Under natural conditions it is presumably always present in sufficient amount. In gardens, especially in old and crowded ones, some of the plants may be benefited by additional supplies (doses) of iron in the soil or otherwise, while others show no need or lack of it.[3] Under the very artificial conditions of water culture, or of other pure culture, considerably larger quantities of iron may be required for apparently healthy life.

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[1] For the literature of the subject consult Molisch, H., *Die Pflanze in ihren Beziehungen zum Eisen,* Jena, 1892.

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[2] Pollacci, G., and Oddo, B., *Rend. Acad. d. Lincei,* 24, 1915; *Gaz. chim. ital.,* 50, 1920.

[3] The story may be found in the literature of the English plant physiologist, Vines, working as a student with Sachs, injecting an iron-containing solution into a chlorotic branch of *Robinia,* in the Botanic Garden at Würzburg, and seeing the leaves turn green. But iron is not a cure for all forms of chlorosis, as we shall presently see.

In these instances the iron must be regarded as a stimulant, a "tonic," rather than meeting the average normal requirement.

The rôles of potassium and calcium in the life of the plant were at one time much more exactly described than is now believed to be possible; for while the absence of one or the other of these elements is followed by certain definite morbid symptoms,[4] we are now much more inclined to consider these symptoms as indicating a profound disturbance of metabolism, perhaps of the protoplasm itself. For example, since the classical work of Nobbe[5] and his associates fifty years ago it has been known that potash deficiency is followed by dulling of the leaf color and by the cessation of the photosynthetic manufacture of sugar and starch and the translocation, from the leaves to places of storage, of the products of food manufacture. One may suspect that the change in leaf color, indicating a difference in the number and wave-length of the light rays absorbed, may be an indicator of the difficulty; but apparently this is not all, if it is really any, of the trouble. Just as no one wheel in the mechanism of a watch may justly be called the most important, but without which the watch will not run properly, so deficiencies in potassium and calcium may be conceived to prevent the proper working of the living mechanism. However, although this analogy may comfort, it should not satisfy, for it is nothing more than analogy.

Hypothesis is offered in place of analogy, and experiment is described as supporting hypothesis. It should be pointed out in this connection, however, as elsewhere, that the living organism, while extremely plastic and therefore able to live under a very great variety of conditions, is not necessarily any better suited by one or another set of artificial as compared with natural conditions. It may get along, *under the conditions of experiment,* better with one rather than another combination, but it might do even better if let alone out of doors.

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[4] Reed, H. S., The Value of certain Nutritive Elements to the Plant Cell. *Ann. Bot.*, 21, 1907. (*Valuable bibliography.*)

[5] Nobbe, F., Schröder, J., and Erdmann, R., *Ueber die organische Leistung des Kaliums in der Pflanze.* Landw. Versuchsstat., 13, 1870.

A great deal of experimental work has been reported on the cultivation of plants of various ages in solutions. In the papers of Livingston, Tottingham, and Shive[6] the literature of the subject may be found. Beyond the point of demonstrating as they have that plants cannot get along without the ten elements previously enumerated, water cultures can be expected to throw only a certain amount of light on crop requirements or other agricultural problems. Apparently different proportions of these ten elements are used during the seedling, growing, flowering, and fruiting stages of wheat, for example; but as there is always at least this much leeway in ordinary soils, it is difficult to see at the moment what the fruit of such experiments is likely to be. In this fact there is no reason for abandoning this line of experiment, for it may well be pursued for its own sake; but if so, no other claim should be made for it.

Thus, it is found experimentally that even pure distilled water is harmful to plants. In addition to the explanations offered by True,[7] experimental investigations by Loeb[8] indicate that the electrical charges of water particles bear a very important relation to their movement through membranes (see pages 27–41), that the charges will vary in sign according to the chemical nature of the membranes, and that the rate of migration of water particles through the membrane will vary with the sign of the charge and with the valencies of the ions of the dissolved substances. Loeb's statement is in regard to the movement of water particles from pure water through a membrane into a solution; but, until and unless warned to the contrary, one naturally extends these conceptions to the movement of water from, for example, the dilute soil solutions through the walls of the root-hairs into the epidermal and other cells of the roots of land plants.

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[6] Livingston, B. E., Further Studies on the Properties of an Unproductive Soil. U. S. Dept. Agric., *Bur. Soils, Bull.* 36, 1907. Tottingham, W. E., A quantitative chemical and physiological study of nutrient solutions for plant cultures. *Physiolog. Researches,* 1, 1914. Shive, J. W., A Three-salt Nutrient Solution for Plants. *Amer. Journ. Bot.,* 2, 1915. A Study of Physiological Balance in Nutrient Media. *Physiolog. Researches,* 1, 1915.

[7] True, R. H., Harmful Action of Distilled Water. *Amer. Journ. Bot.,* 1, 1914.

[8] Loeb, J., Electrification of Water and Osmotic Flow. *Science,* 53, 1921, and references therein cited to *Journ. Gen. Physiol.,* 1918–20.

In a series of papers Osterhout[9] has reported the results of his experiments and his conclusions regarding what he believes to be the antagonistic action of potassium, calcium, and magnesium ions, each of which appears to be poisonous in itself. In what their poisonous properties consist, or by what means they antagonize and neutralize each other, is still a matter of guesswork. They are, however, electrolytes, cations, carrying charges opposite to those of their anions, the acid radicles with which they are united. Furthermore, Loeb found that membranes coated with a film of protein (and all cell membranes are necessarily conceived as being so coated) induce positive or negative charges on the particles of water in contact with them according to the degree of acidity or alkalinity (hydrogen ion concentration) of the solutions. We are, then, ready to entertain with far less surprise than would otherwise be the case, the somewhat startling suggestion of Zwaardemacker[10] that the "use" of potassium, calcium, and

[9] Osterhout, W. J. V., On the importance of physiologically balanced solutions for plants. *Bot. Gazette,* 44, 1907. Antagonism and Permeability. *Science,* N.S., 45, 1917.

[10] Zwaardmacker, H., *Lehrboek der Physiologie,* Haarlem, 1914. See

to a certain extent also of magnesium, ions in or to the plant consists in their properties as electrolytes, influencing, if not largely controlling, the intake of water and the secretion or excretion of water and other substances. Thorough investigation will reveal the accuracy of such a conception. Meantime, we have a welcome suggestion as to the functions of those two elements which apparently do not enter into the structure of living protoplasm, but which are no less indispensable than the other eight.

The idea of Loeb [11] that there exist in the living cell protein compounds of these alkaline elements must also be mentioned in this connection. The importance of such compounds, if they exist, would be indicated by the leaching effect of distilled water. Since it is agreed that distilled water is injurious, part of the harm done by it must be due to the movement of the alkaline elements from the plant into the distilled water bathing its roots. Such movement, ultimately breaking down one or another of the "metal proteids," would correspondingly injure the cell or the plant if such proteids are essential. Similarly, "balanced solutions" tend to maintain, unbalanced or deficient solutions fail to maintain, such "metal proteids" in sufficient amounts and forms.

The organisms living under usual conditions find themselves disturbed by changes in one or another of these conditions; but there are an increasing number of organisms known to live under conditions not only unusual but ordinarily found to be fatal. As we shall presently see, certain organisms live where temperatures are too high or too low (pages 330–331), where light is excessive or lacking (pages 296–329), where water is

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also *Journ. Physiology,* 53, 1920, and Blackman, V. H., Radio-activity and normal physiological function. *Annals of Bot.,* 34, 1920.

[11] Loeb, J., On iron-proteid compounds and their rôle in the mechanics of life phenomena. *Amer. Journ. Physiol.,* 3, 1900.

present only as it is formed by the organisms themselves (*e.g.*, clothes moths, as indicated by Babcock),[12] and where the concentration or composition of the liquids of the environment is fatal to most animals and plants[13] (pages 37–39). One may entertain the idea of "balanced solutions" just as one may entertain any other idea of "balance" in undisturbed nature (*e.g.*, the "balance" between forest and grassland, between squirrels and nuts, between plants and disease); but it is an abstraction, as is the so-called "normal temperature" of the human body, which is only the *average temperature under average conditions*. Under other conditions another balance will prevail. This is obvious from such studies as those of the brine organisms, of the insects on oil and asphaltum seepages, of the fungi on strychnine and other solutions. The proportions of potassium, calcium, sodium, and magnesium ions in concentrated brines are very different from those in fresh or sea water. Most organisms would promptly die in the brines, which may, in fact, be used as preservative liquids for many foods: but nevertheless they have their own fauna and flora, and necessarily a different "balance."

Many attempts have been made, without success, to use compounds of closely allied elements as substitutes. Thus, it is natural to suppose that sodium might, to a certain extent at least, take the place of potassium in plant metabolism. Ordinary experience, however, showing that potassium chloride is not a satisfactory substitute for sodium chloride as table or cooking salt, would lead one to doubt the practicability of such substitution. Owing to their greater cheapness, sodium salts would be very welcome if they would serve as substitutes for potassium salts in fertilizers, but they do not. Sodium salts are extremely useful on certain soils, serving to offset a scarcity of potassium salts but not replacing them.[14] In other instances, the acid radicle rather than the alkaline, is the valuable constituent; and in some instances again, the weak acid radicle may be split off and decomposed, leaving the alkaline to overcome the undesirable acidity of the particular soil.

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[12] Babcock, S. M., Metabolic Water. Univ. Wisconsin, Agric. Exp. Sta., *Research Bull.* 22, 1912.

[13] Peirce, G. J., The Behavior of certain Micro-organisms in Brine. *The Salton Sea*, Carnegie Inst., Washington, 193, 1914.

Sodium chloride, appearing in all ash analyses carefully conducted, may be considered to be indispensible, the more so since many animals are known to suffer if deprived of it. Of nearly universal distribution, its complete exclusion from synthetic culture media is almost unthinkable. Every object touched by human hands receives its trace or more of common salt, each piece of wood contains a trace or more, the air contains suspended molecules of it as dust or otherwise, the containers of culture solutions also contain it and unless extreme pains are taken, even the paraffin or other wax used to coat them for water culture experiments, will contain it too. Indeed, it is more reasonable, as well as easier, to conceive that plants, as well as animals, living in a more or less salty world, are so adjusted to it that it is, to all intent, indispensable. At least, it is practically unavoidable.

On the other hand, certain plants have been supposed to require more than the usual minute quantities of common salt in the soil. Buckwheat, asparagus, and the so-called halophytes or salt plants can be grown, however, with only the usual proportion of sodium chloride in the soil. The enormous production of asparagus on the lands reclaimed by diking in the lower Sacramento and San Joaquin valleys in California is proof so far as this plant is concerned; [15] and buckwheat culture is now generally accomplished without salting the soil. As we shall presently see, the so-called halophytes, or salt plants, and the xerophytes, or desert plants, have many features in common, as indicated twenty years ago by Schimper.[16] These might be conceived to be the results or effects of specific substances or, as Schimper claims and experiment indicates, they are the result rather of the ratio of salts and water, which tend to be alike in the two environments. Cell-sap concentration (see page 38), rather than cell-sap or soil solution composition, seems to be the determining factor in these instances.

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[14] Russell, E. J., *loc. cit.*

[15] Hilgard, E. W., *Soils.* New York, 1906. Wickson, E. J., *The California Vegetables in Garden and Field.* 3d edition, San Francisco, 1913.

Certain features impress one in looking at the plants of salt marshes. In many parts of the world salt marshes are wet, their soil more or less saturated, at all seasons, and bathed in air the humidity of which is always high, except possibly at times in winter when, because the ground is frozen, it is to all intents and purposes dry (see page 62). The marshy shores of parts of the Bay of San Francisco, on the other hand, offer some features strikingly different from those of the Atlantic coast, and correspondingly instructive. They become so dry in summer that they crack; but wet fog may overlie them every night, disappearing only during the forenoon, and the glistening salt crystals on the surface of *Frankenia* during the day may be drops of brine during the night. These plants are dry, small leaved, xerophytic in appearance. So also are the tarweeds (*Hemizonia pungens*). But the *Salicornia*, and the dodder parasitic upon it, are fleshy. The *Frankenia* has little or no salty flavor inside, tarweed has no salty flavor inside or out, and *Salicornia* is salty only inside. Both dry and fleshy plants are here, side by side in many places, but forming zones in others, according to their position with relation to the sea-level. The *Salicornias* are lowest, the tarweeds highest, the *Frankenias* between; but the *Salicornias* do not secrete or excrete the salt, which they would receive in amounts at least equal to those taken up by *Frankenia* if they did. These plants may be grown in soils much less salty. Certain forms of Mesembryanthemum and Stone crop, *Dudleya farinosa* for instance, evidently do not require salt or abnormally high proportions of salts; for they will thrive if the air is dry enough. Halket[17] describes experiments on *Salicornia* and other salt marsh plants which he made in England. The fruits of these experiments should be tested, and if necessary corrected, by researches conducted where, as is indicated above, natural conditions make it possible to distinguish between the effects of the salts themselves in the soil of salt marshes and the effects of very rapid transpiration itself. This conclusion is strengthened by Halket's report as to the condition of the epidermis, stomata, etc., of the *Salicornia* which he studied. Furthermore, the vegetation of the "salt licks," "salt spots,"[18] salt and other "mineral" springs of this country and of the world, offer opportunity for study of this question, provided pains be taken to keep distinctly in mind the possible results of transpiration and of nutrition. This, of course, implies like care in transpiration studies whether of desert or of other plants.[19]

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[16] Schimper, A. F. W., *Plant Geography upon a Physiological Basis.* Transl. by W. R. Fisher, Oxford, 1903. Cowles, H. C., Vol. 2, Ecology, in *Textbook of Botany*, by Coulter, Barnes, and Cowles, New York, 1910.

The practice by farmers, horticulturists, and gardeners of stimulating growth or other plant production by additions to the soil has developed until the idea of fertilizing or manuring the soil is generally familiar. The design of the fertilizer is to supply what is lacking in the soil to give it the greatest productiveness. Often what is lacking is not any mineral or organic matter, but rather due drainage and aeration, which can be furnished by tillage (see pages 48–49). Analyses, physical and chemical, should show the composition of the soil, its excesses as well as deficiencies, and enable the cultivator to add to his soil accordingly. Under usual conditions fertilizers have been obtainable, freely and at reasonable prices. The Great War so dislocated all commerce that fertilizer supply was inadequate and prices were correspondingly high. New sources of supply were called in,[20] some of which may be permanent, others of which were profitable only in emergency. But one of the most important fruits of this war-stringency was the revival of interest, on the part of botanists, in the question of food production and their studies of the requirements of food plants. Obviously one of the main aims of the cultivator is to maintain and if possible enhance the productiveness of his soil, and not merely to stimulate a single crop to maximum productiveness. For this reason the utmost care must be exercised in the use of fertilizer for, at the same time that desired potash is introduced into the soil, there should be no possibility of gradually poisoning the soil with accumulations of borax[21] or other deleterious impurity.

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[17] Halket, A. C., The Effect of Salt on the Growth of Salicornia. *Ann. Bot.*, 29, 1915.

[18] Cannon, W. A., Some Relations between Salt Plants and Salt Spots. *Dudley Memorial Volume*, Stanford University, 1913.

[19] Livingston, B. E., and Shreve, E. B., Improvements in the Method for Determining the Transpiring Power of Plant Surfaces by Hygrometric Paper. *Plant World*, 19, 1916.

While the laboratory researches of Richards[22] and many others [23] have shown that boron, copper, zinc, and other elements act and may be used as stimuli, experience shows that their use is dangerous or damaging in practice. In fact, the interested coöperation of botanists, particularly of plant physiologists, in the studies of chemists and others engaged in agricultural work is called for not only by the self interest of food-consuming individuals in a hungry world, but of devotees of a science which can prosper only as it shows itself to be meeting human needs. The so-called " exhaustion " of the soil in various parts of this new country is sad commentary on our intelligence. The " worn out " soils of New England are not now so badly handled, though they undoubtedly have been. In view of the enduring fertility of the farms of northwestern France and of the highly cultivated parts of Asia,[24] it is obvious that one of the problems of first importance in this country is the treatment of our soils so that they will not wear out or run out or otherwise deteriorate. Cameron and others [25] have shown that in certain " exhausted " soils the trouble consists rather in accumulated " toxic or inhibitory organic substances, whether excreted by roots or otherwise produced " and not at all in exhaustion. As previously pointed out (page 99) suitable crop rotation will avoid this difficulty. It will, furthermore, give opportunity for the continuance of those processes of weathering, and of soil-working by worms, ants, fungi, and bacteria, upon which the natural production and maintenance of the soil and its components depend. In fact, careful study of the means employed by older races in maintaining soil-productiveness is of increasing importance. With the increase in population and the corresponding decrease in the productive area of the earth's land surface, the maintenance at least, and if possible the increase, of productiveness becomes more and more necessary. While plant breeders may confidently be expected to give us strains more resistant to disease and more prolific, these same plants must be nourished in the soil. Revision downward of our scheme and scale of living, which is frequently threatened by economists and sociologists, can be postponed, if at all, only by such permanent improvement of production as shall conserve the power of production at the same time that it increases the fecundity of the plants cultivated.

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[20] See Fertilizer Resources of the United States, *Sen. Doc.* 190, 62nd Congress, 2nd Session; and Turrentine, J. W., and Shoaff, P. S., Potash from Kelp, *Journ. Indust. and Engin. Chem.*, 2, 1919.

[21] Cook, F. C., and Wilson, J. B., Boron: Its Effects on Crops and its Distribution in Plants and Soils in Different Parts of the United States. *Journ. Agric. Research*, 13, 1918.

[22] Richards, H. M., Die Beeinflussing des Wachsthums einiger Pilze durch chemische Reize. *Jahrb. f. w. Botanik*, 30, 1897.

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[23] Drechsel, O., Zur Kenntniss der sogenannten Oligodynamischen-Erscheinungen. *Centralblatt für Bakteriologie,* II, 53, 1921.

[24] King, F. H., *Farmers of Forty Centuries: or Permanent Agriculture in China, Korea, and Japan.* Madison, Wis., 1911.

[25] Cameron, F. K., *The Soil Solution: The Nutrient medium for Plant Growth.* Easton, Pa., 1911. Schreiner, O., and Reed, H. S., Schreiner and others in *Bulletins,* Bureau of Soils, U. S. Dept. Agric., 1907 to date.

VI

THE MOVEMENTS OF WATER

The absorption of water and dissolved substances by the plant from the media — soil, water, air — in which it lives is accomplished under principles and by forces as fully discussed in the foregoing pages (19–41) as our space permits. Reflection will promptly show that absorption, for example by root-hairs from the surrounding soil, must take place from cell to cell, elsewhere in the plant body, whenever the physical conditions make this possible. A root-hair is a bag of water, consisting of one or more membranes of different degrees of permeability to different substances dissolved in the water which comes into contact with the membranes. The cell adjoining a root-hair is also a bag of water consisting of membranes of protoplasm, the celluloses, etc. Furthermore, the aqueous solution, within a living cell, whether gathered into a vacuole or not, permeates the protoplasm and its products, including the cellulose walls. Thus living cells are not only bags of water but the walls of the bags are also wet. Wherever such wet walls touch water, whether the water be the soil solution or the solution in the wall of the next cell, the two volumes of water will unite at the areas of contact. Hence movements will take place at and across these areas of contact. These movements will transfer water and the substances in solution from cell to cell throughout the body of a multicellular plant or animal wherever cell contacts make such dialysis possible.

Examination of plant and animal bodies shows that the cells forming these bodies, though in contact with each other, and thereby forming parts of a continuous mass of water, are not compact. There are intercellular spaces; cells elsewhere in contact with each other along their periphery do not touch everywhere. In plants these intercellular spaces may communicate with each other and with the outside air, as the cavity of the human lungs communicates with the air, which thereby is made continuous within and without the chest. Though diffusion may, indeed must, take place along these intercellular spaces, only water vapor, other vapors (*e.g.*, volatile oils), and gases will diffuse along them.[1] There will be no movement of liquid water along them; they are not aqueducts. The movement of water, and of such substances as may be absorbed by roots from the soil, must take place, therefore, from cell to cell across the areas of contact, by dialysis, in obedience to those same physical laws controlling their entrance into any part of the body.

The relatively low solubility of oxygen in water, as compared for example with carbon dioxide,[2] makes the maintenance of communicating and air-filled intercellular spaces, or of a circulatory system (the blood) necessary if the plant or animal body is to attain any but the smallest dimensions. But if gas exchange by diffusion be facilitated by large intercellular spaces, the movement of water and the dissolved ash constituents (pages 120–132) by dialysis, confined to the areas of contact of cell with cell, will be correspondingly limited. Plants and animals living submersed are assured of a supply of water ample for every need — as food material, the medium of movement of food materials and foods, etc., etc. — but plants and animals living on land lose water by evaporation. Many factors regulate the amount and the rate of loss by evaporation,[3] and the structural and other relations of plants to this inescapable phenomenon are the objects of study and report of anatomists and ecologists, as well as of physiologists.[4] In dry air the loss will vary with the temperature; and the loss will vary with the dryness. The loss by evaporation takes place at the area of contact of the air and the wet cell surfaces. These areas of contact are extensive or limited, superficial as in the filmy ferns or only internal as in ordinary mesophytes, in plant bodies large and multicellular,[5] according to the kind, size and solidity of the plants and according to the temperature, dryness and movements of the air, and the amount of water available for absorption. Thus the vegetation of moist tropical, humid, semi-arid, and desert regions exhibits in the anatomical arrangement and in the composition of the parts of the bodies of its plants, the resultants of the forces and conditions amid which these plants live. The surface of the plant body in contact with the air, including the surface of its component cells bordering on intercellular spaces, is large or small according to air humidities and temperatures and to the available water supply, the bodies of desert plants being compact, limited in surface, solid in structure, and with waterproof coverings, while those of the tropical " rain-forests " are large, diffuse, and porous.[6]

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[1] In this connection as well as later, it may be well to mention that, in a considerable number of plants, water storage takes place in intercellular spaces (see Haberlandt-Drummond, *Physiological Plant Anatomy*, p. 409), or intercellular spaces at the ends of bundles or elsewhere may fill with water under certain conditions.

[2] The relative solubilities of O_2 and CO_2 in water at 20° C. and atmospheric pressure are as 1:2.83 by volume, *i.e.* that, under these conditions, nearly three times as much CO_2 will dissolve as oxygen.

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[3] See Cowles, H. C., Ecology, Vol. II of *Textbook of Botany,* by Coulter, Barnes, Cowles, New York, 1911.

[4] C. V. Piper's paper in *Science,* N.S. 53, Mar. 25, 1921, pleads for what most botanists have long recognized, namely, that agriculture, forestry, horticulture, agronomy, etc., are merely special fields of botanical endeavor, different from but no less scientific in aim and conduct, other things being equal, than taxonomy, cytology, paleophytology, etc. What most botanists have failed to recognize is the intellectual stimulus and the material advantage of cordial understanding coöperation among the different kinds of persons interested in plant studies. Would animal physiology have received the support which has made possible its gratifying development if it had insisted upon ignoring human needs and human interests?

[5] Dixon, on the first page of his valuable monograph on *Transpiration and the Ascent of Sap* (London, 1911), indulges in an interesting but misleading calculation. From this he concludes that "the combined area of the stomata is at least ten times as efficient in giving off water vapour as a free water surface of equal area." As a matter of fact *no water* is "given off" by the stomata; they are simply the gates through which water vapor, already "given off" into the air by dialysis through the very extensive areas of cell-surfaces bordering the air-filled intercellular spaces, diffuses out of the cavities within the body of the plant and may under certain conditions be said to flow out. The stomata must be regarded merely as faucets or dampers controlling the flow of water vapor already evaporated. The distinction attempted and perpetuated by the

The familiar phenomenon of wilting, whether taking place from small parts cut off from the rest of the plant or from larger leafy flowering branches, reveals the inadequacy of any system of water supply depending only upon dialysis through cell contacts; for even branches, provided with wood, and leaves with veins, wilt though cell contacts are unimpaired.

Many experiments[7] have established beyond question the

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continued use of the term transpiration is, I believe, false; for evaporation, while *revealing* itself at or above the surface of the plant, has already taken place within it. And it will proceed, slowly or rapidly, according to the volume, temperature, and dryness of the air of the intercellular spaces in relation to the cells bordering the spaces. If by transpiration is meant this flow through stomata it might be well to retain the term, if it were possible to distinguish this from the evaporation which, though in many instances slight, actually takes place through the whole surface of the plant body exposed to air. Attempts to show that cuticular evaporation is *nil* are bound to fail, though they demonstrate its slowness in many cases.

[6] See Schimper's *Plant Geography* and the other descriptive works of the ecologists.

[7] For the literature see Dixon, H. H., *Transpiration and the Ascent*

fact that, in the vascular land plants, water ascends in and through the wood elements, ducts and tracheids, from the roots to the leaves and other parts, from which it is lost by evaporation. Between the imperfectly conducting tracheids of the wood of the *Coniferæ* and the remarkable conducting power of the wood of *Eucalyptus*, oak, the leaves of the tropics, and the vines of the *Cucurbitaceæ*, there are all gradations. Differences in the amount and position of the wood, as well as in its own conducting power, must be recognized. And when all available anatomical information is secured, and experiment is resorted to to determine the means of sap ascent, candor compels us to admit that little is actually known of this very evident and much studied phenomenon.

A leaf spread out as one of many, a hundred feet above ground in the air, is bound to dry and die unless duly supplied with water. Such supply goes up through ducts and tracheids mainly, regulated in rate by the loss and use of water in green and other tissues. Microscopic examination shows direct contact of living cells — *i.e.*, dialyzing systems — with the ducts and tracheids, dead shells of cells, of the wood, a sufficient number of such living dialyzing systems touching each duct and tracheid to supply it with water, or take water from it, according to the osmotic pressures prevailing in each particular part of the plant. From this, as well as from other considerations, many persons besides Godlewski[8] have felt constrained to believe that the living cells

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of Sap. London, 1911. Nordhausen, M., Weitere Beiträge zum Saftsteigeproblem. *Jahrb. f. w. Bot.*, 60, 1921. Renner, O., Versuche zur Mechanik der Wasserversorgung. *Ber. d. d. Bot. Ges.*, 36, 1918. Bode, H. R., Beiträge zur Dynamik der Wasserbewegung in den Gefässpflanzen. *Jahrb. f. w. Bot.*, 62, 1923.

[8] Godlewski, E., Zur Theorie der Wasserbewegung in den Pflanzen. *Jahrb. f. w. Bot.*, 15, 1884. Nordhausen, M., *loc. cit.* Renner, O., *loc. cit.*

adjoining the ducts and tracheids furnish the lifting power which carries water up the stem. The mechanics of this supposed pumping action are as difficult to visualize as it is unnecessary to conclude, from the fact that living cells do touch dead ducts, that the living cells do more, in the matter of water transfer, than maintain the indispensible dialyzing systems. When, in the experiments of Strasburger[9] and others, poisonous solutions are employed, it is clear that no cell is hurt, either as to its actual permeabilities or as to its supposed pumping action, until the poison reaches it. Furthermore, though one may presumably kill all the cells in a given zone by the application of sufficient heat,[10] neither the activities nor the permeabilities of the cells above and below will be immediately affected, and the heat, even if not fatal to all the cells, may cause precipitations. These precipitations, demonstrated in certain instances[11] as plugs in the vessels or in the pits in the walls, correspondingly interfere with sap ascent.

That the living cells in plant organs have much to do with the rate of water movement and water loss is evident both from certain reflections and also from certain experiments. As intimated above, living cells constitute dialyzing systems, the characters or qualities of which depend both on the composition of the solutions in contact with the membranes and upon the permeabilities and impermeabilities of the membranes themselves. The permeabilities of cell membranes are altered by many things; but the changes induced by abnormal temperatures, by poisonous irritants, and by death must be considered much more definitely than they seem so far to have been in studies of water movement in plants. The following facts bear upon this particular matter.

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[9] Strasburger, E., *Ueber das Saftsteigen*, Jena, 1893.

[10] Overton, J. B., Studies on the Relation of the Living Cells to Transpiration and Sap Flow in Cyperus. *Bot. Gaz.*, 51, 1911.

[11] Weber, C. A., Ueber den Einfluss höherer Temperaturen auf d. Fahigkeit des Holzes den Transpirationstrom zu leiten. *Ber. d. deutsch. Bot. Ges.*, 3, 1885.

The surface of ordinary leaves is formed of a single layer of epidermal cells the outer walls of which are more or less waterproofed (cutinized). This layer is interrupted at very short intervals, the clefts or openings being bounded by cells unlike those forming the rest of the epidermis. These peculiar cells differ in form, size, attachment to their neighbors, in thickness of walls and in contents. In most plants these clefts, *stomata,* are opened and closed by the changes in form of the bordering *guard-cells,* which, unlike the other epidermal cells, contain chlorophyll. The classical studies of von Mohl and Schwendener[12] have demonstrated the mechanics by which stomata are opened and closed; but it is not yet agreed what influences control and operate the mechanism.[13] The stomata open and close by reason of changes in the turgor of the guard-cells. When the concentration of their cell sap rises, water is absorbed, if possible, from adjacent cells, the turgor increases, the walls of the guard-cells are correspondingly stretched, and the form of the guard-cells is thereby changed from roughly ellipsoidal to roughly spheroidal. Thus the cleft or slit or opening in the epidermis is made or widened as the guard-cells separate. When the turgor falls the cell walls are less stretched, the guard-cells flatten, the adjacent

[12] Mohl, H. von, Welche Ursachen bedingen die Erweiterung und Verengung der Spaltöffnungen? *Bot. Zeitung,* 1856. Schwendener, S., Ueber Bau und Mechanik der Spaltöffnungen, *Monatsh. d. Preuss. Akad. d. Wiss.* Berlin, 1881.

[13] Darwin, F., *On the Relation between Transpiration and Stomatal Aperture.* Phil. Trans., London, Ser. B, 207, 1916. Lloyd, F. E., The Physiology of Stomata. *Carnegie Inst.* (Wash.) *Pub.* 82, 1908. Gray, J., and Peirce, G. J., The Influence of Light upon the Action of Stomata and Its Relation to the Transpiration of certain Grains. *Amer. Journ. Bot.,* 6, 1919.

faces of the pair approach or come into contact with each other, the slit narrows and closes. But what makes the turgor rise and fall?

The epidermal cells of most land plants have chlorophyll grains (chromatophores) only in the guard-cells of the stomata. In shade plants of many different species and families, but especially, perhaps, the ferns, as distinct from plants of the open, chlorophyll is more or less developed in all the epidermal cells. In some of these too the upwardly bulging form of the epidermal cells may assist in receiving and concentrating the more or less deficient light required for photosynthesis.[14] But in plants so placed that their leaves can receive and absorb the normal amount of light, the chlorophyll in the palisade and mesophyll parenchyma can absorb enough light to convert into sugar the carbon dioxide and water which reach them, and the ordinary epidermal cells do not make sugar. The guard-cells, on the other hand, at least in stomata which open and close, can rapidly increase the density of their cell sap in daylight, if they contain chlorophyll, by making sugar. Increase in the density of the cell-sap will be followed, if possible, by absorption of water from adjacent cells. Thus the guard-cells, attached to the neighboring epidermal cells but not attached to each other throughout the whole length of their proximate faces, can separate or squeeze together according to their state of turgescence. No such change is possible in cells incapable of sugar manufacture; but it is possible in these only in the light. On the other hand, if ordinary epidermal cells contain starch, digestion of this starch, resulting in sugar formation, will affect their turgor also; but starch is not abundant in ordinary epidermal cells.

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[14] Haberland, G., transl. by M. Drummond, *Physiological Plant Anatomy*. London, 1914, pp. 616, *et seq.*, where he discusses papillose epidermal cells among " the optical sense organs of foliage leaves." The opposite is seen in those plants the stomata of which are sunken below the surface, as is commonly the case in desert plants (see Haberland-Drummond, p. 461).

The facts called for by the foregoing theory have been very imperfectly established, although recent evidence in favor of the theory supplements and strengthens the older. Thus Wiggans [15] and Ilgin [16] report determinations of the density of the cell-sap of the guard-cells not only in comparison with that of other epidermal cells, but also at different times in the day. Wiggans claims that the osmotic concentration in the guard cells increases in the early hours of the day, declining in the latter part of the day, exceeding the concentration of ordinary epidermal cells during the hours in which the stomata are open, and that changes in the concentration in ordinary epidermal cells are slight. It is obvious that further studies of this sort, extended to plants of different regions and conditions, may lead to very significant conclusions.

It is obvious that guard cells containing starch and sugar can control their turgor by digesting the starch or converting the sugar into starch. Thus digestion, and its opposite, storage, by raising and lowering the concentration of the cell-sap, will also raise and lower turgor, opening and closing the stomata.

The guard-cells of stomata differ still further from ordinary epidermal cells, according to the observations of Strasburger [17] in not being connected with their neighbors by strands of cytoplasm passing through their walls. They are, in this respect also, more independent than other component cells of the plant body.

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[15] Wiggans, R. G., Variations in the osmotic concentrations of the guard cells during the opening and closing of stomata. *Amer. Journ. Bot.*, 8, 1921.

[16] Ilgin, W. L., Die Regulierung der Spaltöffnungen mit der Veränderung des osmotischen Druckes. *Beih. Bot. Centralb.*, 32, 1914.

[17] Strasburger, E., Ueber Plasmaverbindungen pflanzlicher Zellen. *Jahrb. f. w. Bot.*, 36, 1901.

The position of the guard-cells, which are often more or less sunk below the general level of the epidermis, protects the stomata from many hazards. While they are common paths of infection by parasitic fungi,[18] and by bacteria as well,[19] and while they ultimately clog even in clean dry air, as is shown to be the case on the old leaves of pines, etc., they are less likely to be sealed by dew and rain, or stopped by dusts, than if they projected above the general epidermal surface or were even with it. As we shall presently see (pages 52, 178), the stomata are also the principal gateways of gaseous exchange between the atmosphere and the air of the intercellular spaces, and as such should be kept free to open and close, and to permit intercellular movements (diffusion) of carbon dioxide and oxygen, and even molar movements. In most land plants, the leaves of which are more or less horizontal in position, the stomata are more numerous on the under side than on the upper, if not limited to the lower side. Hence the risk of closure by rain and dew is diminished. In the case of pendent leaves, with stomata on both sides, rain and dew do not adhere. In fact, owing to the cutinization or the waxy coating of the outer wall of epidermal cells, water does not spread over them but stands, or falls off, in drops. But atmospheric dusts, such as soot, road dust, and dust from cement manufactories,[20] may collect in such amount as to clog or cover, and so impair the efficiency of stomata.

The possession of chlorophyll renders the guard-cells of the stomata more sensitive to atmospheric pollutions than cells which contain no pigments easily affected by acids. This has been observed in the course of my smelter work, both in the field and in the experiment house,[21] and is especially important where plants are living under conditions in which the supply of water is limited and its conservation important. This will be referred to again later (pages 83, 144 ff.).

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[18] Duggar, B. M., *Fungous Diseases of Plants.* Boston, 1909.

[19] Smith, E. F., *Bacterial Diseases of Plants.* Philadelphia, 1920.

[20] Peirce, G. J., The Possible Effect of Cement Dust on Plants. *Science,* 30, 1909. An Effect of Cement Dust on Orange Trees. *Plant World,* 14, 1911.

Because stomata are so evidently able to reduce the loss of water from leaves by closing, it has long been supposed by many persons that their opening and closing are determined by the amount of water in the plant, that when there is enough water the stomata open, when there is too little they close; and that, when a certain degree of wilting is reached, they may inevitably open again, and thus lose control of evaporation or transpiration. This guess seems strengthened by the possession of motionless guard-cells and constantly closed stomata by certain submersed aquatics, and by constantly open stomata in many plants living in swamps and swampy places. Of the latter sort the willows are perhaps the most noteworthy. But apparently many other than the swamp plants have constantly open stomata,[22] though it might be conceived to be to the advantage of some of these to be able to close them. In fact, one may wonder, in spite of the great amount of study which has been devoted to them, and of their undeniable importance, whether their present value may not be less than in earlier geologic time. Under the then prevailing conditions, possibly of more intense light, greater proportions of carbon dioxide in the air, and perhaps higher or lower humidities, there may have been stimuli which could have developed structures too elaborate and too delicate to be fully understood under current conditions.

On the other hand, it is evident that cells containing chlorophyll will be acted upon by light in other ways than those lacking it, and it is evident that their protoplasm is especially sensitive to light. Direct observation of stomata in place, on leaves undisturbed except that, while still attached to the plant, they are so moved that they can be examined through a microscope, shows [23] that stomata open and close according to the increase and decrease in the intensity of illumination. It may well be in this case, as in many others (pages 313 ff.), that rays of light of definite wave-lengths stimulate the guard-cells and thus induce the opening, but experiment has not tested or illuminated this suspicion. But the various methods employed by Darwin,[24] Lloyd,[25] and many others,[26] show that the stomata are open in light, closed in darkness, and control evaporation (transpiration) as well as gas exchange accordingly. Whether this control of transpiration is of major or minor importance in any particular instance seems to be dependent upon the kind of plant and the nature of its environment. It is obvious that plants forced to operate with the maximum economy of water, as is the case in arid and semi-arid regions, where irrigation and "dry farming" are applied to cultivated plants, and where low humidities prevail, at least during the sunny hours, are in very different case, as well as being in many instances themselves very different, from those in well watered regions and where the humidity of the air is generally high throughout the growing season.

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[21] See Willstäter and Stoll, *Chlorophyll.* Berlin, 1913.

[22] Haberlandt, G., transl. by Drummond, *l. c.*, pp. 474, *et seq.*

That the transpiration of wheat and barley in the grain fields of the semi-arid west is greatly influenced by the condition of the stomata is evident to any one who has observed the conditions of the foliage of plants subjected to sufficient doses of sulphur dioxide to affect the guard cells. In the literature treating the influence of smelter fumes on vegetation certain authors claim, and others dispute or deny, that there are

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[23] Gray and Peirce, *l. c.*

[24] Darwin, F., *l. c.*

[25] Lloyd, F. E., *l. c.*

[26] Literature cited by the above and by Gray and Peirce, *l. c.*

"invisible" injuries.[27] These show themselves in part in subnormal growth (pages 84–86); but in the present connection I may point out the dryness of the leaves of affected grain plants in contrast to the normal moistness of unaffected foliage. This difference appears in different parts of the same blade of wheat. Microscopic examination betrays the cause; for the guard-cells of the stomata are more or less brown and more or less open over the dry parts, normally green over the normal parts. More extended examination, both in time and in the area of leaves under examination, shows that browning of the guard-cells precedes their failure to close and the drying out of the leaf. This conclusion is confirmed, furthermore, by experiment; for a leafy branch of *Eucalyptus* exposed to a dose of 3 parts SO_2 per million parts of air for a brief time (say 15 minutes or less) will transpire more rapidly than before and than comparable undosed control branches. This particular line of experiment has, however, barely been entered upon; but for the information which it may yield regarding the condition of shade and ornamental trees in streets and parks of cities, and the means of ameliorating their condition, it should be pursued. It must be pointed out, to the discomfort of many experimenters in Europe and elsewhere, that the experimental study of air pollutions can be prosecuted only where the air is entirely free from other pollutions than those deliberately produced. We scarcely realize that urban dwellers live always in bad air, the badness of which is due, not to carbon dioxide but to sulphur dioxide, soot and other dirt from coals and oils used as fuels, and to illuminating gas distributed through leaky pipes.[28]

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[27] See the *Report of the Selby Commission, Bull.* 98, U. S. Bureau of Mines. Washington, 1915.

[28] In a suit decided in Salem, Massachusetts, in 1921, the Court estimated the value of five old street trees killed by gas escaping from leaky pipes in the ground and assessed damages against the Gas Company at

We have thus seen (pages 19–41) the means and the manner of absorption of water, and of dissolved substances, by the roots of land plants, through root-hairs in contact with soil particles covered with films of soil water, a dilute solution of mineral and possibly other matters; and we have also seen the inevitable loss of water from the leaves and the rest of the parts of land plants in the air, a loss more or less controlled and reduced by waterproofing (cuticula, cork, hairy or waxy developments) and by the closing of the stomata, guarded openings through the epidermis (pages 52 ff.). The quantities of water lost have been measured with increasing accuracy, and still ideas as to the really great quantities given off are vague and entertained by few. Yet one may reach approximate notions of the quantities in several ways. Let us consider as an example, the immediate neighborhood of Stanford University, where the average annual rainfall is only about 15 inches. This means one and one quarter cubic feet, 9.375 gallons, or 78.125 pounds, of water per square foot of area. Assuming that a city lot has an area of 50 x 120 = 6000 square feet, the weight of water falling upon it in a year is about 468,750 pounds or 234.375 tons. There are about 300 acres in the Arboretum of Stanford University. The total weight of water falling upon the Arboretum is then over 500,000 tons per annum. Trees and shrubs are the plants there cultivated, the herbaceous vegetation consisting only of the weeds which grow during the rainy season (winter) and are cut down and followed by a carefully prepared dust mulch for the dry season. Of the annual rainfall by far the major part falls to the

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$200 per tree. See also Crocker, W., and Knight, L. I., Effects of Illuminating Gas and Ethylene upon Flowering Carnations. *Bot. Gazette,* 46, 1908. Knight and Crocker, Toxicity of Smoke. *Ibid.,* 55, 1913. Harvey, E. M., Some Effects of Ethylene on the Metabolism of Plants. *Ibid.,* 60, 1915.

ground and, as the area is flat, would soak in but for the ditches, roads, and gutters required for public convenience. An unknown but variously estimated (guessed) fraction, clinging to foliage and bark, evaporates directly into the air. Let us assume this to be one third, 3.125 gals. or 26.04 lbs. What would happen to the other two thirds if there were no run-off? Soakage and immediate evaporation would account for this. Let us cut off one sixth of this as amply covering evaporation from the surface of the soil during and immediately after rain. Then 6.251 gals. 43.4 lbs. of water will soak into every foot and a total of 283,594 tons will soak into the soil of the Arboretum per season. The soil of the Arboretum being underlain by hard-pan, the imperviousness of which to water, moving upward or downward, is generally known to farmers and horticulturists, we can ignore any additions to the soil water from below; and as the surface of the hard-pan is practically horizontal, we can also ignore any run-off along the line of contact between it and the upper soil. Most of the water soaking into each square foot of soil will, therefore, remain there for a time. But, as everyone observes, soil dries, or is dried by air and by the vegetation which it supports. The beneficial results of the high winds of early spring in drying the surface of soil sodden by melting snow or by heavy rain are evident; but subsequent soil cultivation is designed not only to facilitate root growth, and the absorption of food materials, but also to check drying. The effectiveness of a dust mulch in conserving soil moisture has been already referred to (page 100). Granting, then, the effectiveness of a dust insulator, it is evident that the major part of what falls as rain upon every foot of soil must be returned to the air before the beginning of the next rainy season, else the area in question would presently become a swamp, a lake, etc. The return of this great tonnage is accomplished by the trees, shrubs, and herbage, which lift the water absorbed by the root hairs through the roots, trunk, branches, and distribute it to the leaves from which it escapes into the air.

To continue our illustration, if we assume that a well developed and vigorous geranium plant occupies one square foot of soil in the Stanford Arboretum it will have six and a quarter gallons or forty-three and four tenths pounds of water to draw upon for the year. It will not continue to thrive on such proportion of this as it can secure, it will stop growing and it will lose leaves, but it will not die. If given due amounts of water in addition, it will thrive. In other words, one geranium will require more than the fraction of six and a quarter gallons or forty-three and four tenths pounds of water which it may be able to absorb from increasingly dry soil. What this fraction is may be determined; but for the purpose of this illustration, the exact amount, which would vary from plant to plant, does not matter. The point is to secure a graphic idea of the very large quantities of water absorbed by the roots, lifted through the stems, and lost through the leaves of land plants.

The work of Briggs and Shantz, and of the investigators cited by them,[29] has yielded measurements of the amounts of water required by various crop plants and has shown very plainly that the same species or variety under unlike conditions, such as may develop in successive seasons on the same spot, as well as in different places or regions, will require, use, and lose different amounts of water. Thus they found that, to raise alfalfa in Akron, Colorado, requires roughly 1000 grams of water per gram of dry weight of crop. Briggs and Shantz's figures for the three crops in the growing season of 1911 are interesting because they show the influence of external conditions (weather, etc.) on the same plants; thus the average water requirement for the first crop, mid-May to mid-July, was 1,008 ± 26 grams of water to 1 gram of crop, for the second crop, mid-July to mid-September, 1,354 ± 22 grams of water, for the third crop, mid-September to late October, 520 ± 9 grams, or a mean of 1,068 ± 16 grams of water to 1 gram of crop air-dry. The mean of two crops of sweet clover was 709 ± 9 grams of water to 1 of crop. One crop of Canada field peas required 800 ± 17 grams of water to 1 of crop. The mean of four varieties of oats was 614 grams, of four varieties of barley 539 grams, of five varieties of wheat 507 grams, and of two varieties of millet 275 grams. When one compares the total water requirements with the grain produced the figures are somewhat different. Canada field peas and rye require nearly one and two thirds times as much water as wheat, oats one and a quarter times as much, while millet requires about two thirds and sorghum a little over one half as much water to produce a gram of grain. The same investigators show that different varieties of the same species have different requirements under the same conditions. Thus nearly or quite 600 grams more water per gram of grain are required by "marvel bluestem" than by "Emmer" wheat.

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[29] Briggs, L. J., and Shantz, H. L., The Water Requirements of Plants. *Bull.* 284, *Bureau Plant Industry*, U. S. Dept. Agriculture, 1913. *Bull.* 285, *Bureau Plant Industry*, U. S. Dept. Agriculture, 1913. Relative Water Requirements of Plants. *Journ. Agric. Research*, 3, 1914.

The value of these and similar determinations to agriculture is evident. The differences even among varieties, indicating the greater fitness of one over another for a particular environment in semi-arid regions, show also the desirability of breeding still other varieties, equal in fruitfulness but excelling in the modesty of their water requirements. Given the minimum quantities of water required, semi-arid regions offer, as we shall presently see (pages 305–314), certain remarkable advantages, the value of which is not yet fully realized either in theory or in practice.

Deferring for the moment any consideration of the changing rates at which water is lifted and lost, we may inquire as to the means of lifting it. As previously pointed out, the root-hairs and all other living cells intervening between the soil and soil water on the one side and the ducts or tracheids in the wood of the roots are osmotic systems, unequally permeable to the different solutes. The ducts and tracheids, dead shells merely, are not osmotic systems, though bordered by such. They are, therefore, incapable of developing such pressures, partial or total, as living cells or other osmotic systems, and conceivably the cells may, while discharging water into them, retain one or another solute. Under certain conditions the water in the woody tissues may be a rich solution, as we shall presently see to be the case in sugar maple trees in the spring (see pages 168–173); but at other times it is apparently nearly or quite pure. The resort by travelers, parched with thirst, to the fleshy tissues of certain plants as a source of drinking water[30] illustrates the dialyzing action of the osmotic systems bordering the conducting, and forming the water-storing, tissues of these plants.[31]

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[30] *The Palm Tree Cup.* In October, 1912, I was riding in the plains which are traversed by the upper Paraguay river and its tributaries, in about latitude 10 degrees south, and having become thirsty asked my companion, a Bolivian Indian, if it were possible to find any water fit to drink. The plain was marshy and the pools, although numerous, were both warm and uninviting. Alligators' snouts stuck from among the pads of the great Regina water lily, and every kind of swimming or crawling creature swarmed up when the water was disturbed.

The Indian turned to where the ground was slightly higher and supported a growth of palm trees of moderate height. Beside one of them grew a young shoot which ended in a closely wrapped spathe. He cut off the top of the spathe with a stroke of his machete and scooped out the inside, leaving a goblet-shaped cup, which was green without and white within. In a moment it filled with a clear liquid, which he drank. When the cup had refilled itself, he invited me to do likewise and I found the liquid deliciously cool and satisfying. It had a slightly acidulated taste and a very slight mucilaginous quality. The cup filled again as I turned away and would, I suppose, have quenched the thirst of as many as might have drunk from it until in the course of hours or days the sap ceased to flow. — Kindly communicated by Professor Bailey Willis, Stanford University.

It has long been known that the major part of the water moved from roots to leaves traverses the wood. The disputes over the parts of the wood — walls, as claimed by Sachs,[32] cavities of the ducts and tracheids, as now generally conceded — have led to agreement that water moves upward through the tubes of the vascular bundles which form the wood of the roots and stems and the veins or nerves of the leaves. Anatomical study of the wood or xylem portion of the vascular bundles has thrown only too little light on the mechanics of water movement.[33] Certain things probably are so plain as to conceal the rest. Thus ducts and tracheids form continuous systems. But observations disclose that neither the systems, nor the ducts and tracheids themselves, are filled at all times and perhaps not at any time, with continuous columns of water. Instead, while the mass of water in a plant may be continuous, it may contain bubbles of air or other gas. The water is continuous in a mass of soap-bubbles, its thicker parts connected by films around the air bubbles. In ducts and tracheids these films may coat the inner surface of the walls, in addition to being in the wet walls themselves. The dimensions, composition, and configuration of the inner surface of the walls of

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See also Copeland, E. B., *The Coco-nut,* 2nd Edition, New York, 1921, in which he gives the volumes of sap derived, not for immediate drinking but for wine-production. Molisch, H., *Populäre biologische Vorträge,* pp. 173 *et seq.,* Jena, 1920, and the literature there cited. Maiden, J. H., Australian Vegetation. *Federal Handbook on Australia,* p. 173, Melbourne, 1914.

[31] See Haberlandt's *Physiological Plant Anatomy,* p. 397.

[32] Sachs, J. von, Ueber die Wasserbewegung im Holz. *Arb. d. Bot. Inst. in Würzburg.* Leipzig, 1888.

[33] Strasburger, E., *Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen.* Jena, 1891.

ducts and tracheids offer certain resistances to the passage of liquid water. This resistance is the same in one direction as the opposite, within short distances or between nodes or joints; but the anastomosis of the vascular bundles at the nodes, and the branches to twigs, leaves, etc., offer unequal resistances upward and downward, though there are no evident valves as in the vascular systems of higher animals. In any case, to lift a pound of water one foot in the air requires an amount of energy sometimes spoken of as a foot-pound, or 0.3240 gr. calories. To lift this water the same distance through a conducting system requires this amount of energy plus that necessary to overcome the resistance of the system. This resistance, consisting in friction, filtration, and perhaps other factors, is stated by Dixon [34] to be "approximately equivalent to a head of water equal in length to the wood traversed." This then doubles the force required to lift water through the stem or trunk.

In the literature capillarity, osmotic pressure, gravity, gas pressure, sap or root pressure, and the pumping action of living cells, have all had their advocates. The experimental evidence in favor of each has proved inadequate.[35] Reflection will show that capillarity must be involved, but that it alone cannot move the water in sufficient volume from the source to the place of loss. This may be considered in connection with the paper by Copeland, who constructed an artificial tree and leaf by filling connected glass tubes with Plaster of Paris. The plaster column 12.4 meters long he steeped in water, topping it with a cup of plaster impregnated with potassium ferricyanide, covered by parchment paper, similarly impregnated, and holding a concentrated solution of salt and copper sulphate. Water ascended this column. In the first place Plaster of Paris, which sets with 18% of water, will finally absorb up to 32%, there being two molecules of water of crystallization to each molecule of crystallized calcium sulphate.[36] This will account for a continued and very considerable current of water upward through the mass. In the second place, capillarity will act in this column of Plaster of Paris as it obviously cannot for anatomical reasons in ducts and tracheids of wood. Finally Copeland's conclusion that "the rise of water to make good the loss by transpiration is due to the pressure of the atmosphere, or to this and other forces coöperating with it and regulated by it" is based on the indefensible assumption that the upward pressure of the atmosphere at the base of every plant is not almost perfectly balanced by the equal downward pressure at the top. In other words, unless one can assume that ducts and tracheids, either singly or as systems, constitute barometer tubes, with a Torricellian vacuum at the top of each, the "pressure of the atmosphere" must be eliminated from consideration in this connection. Furthermore, it can apply, at the best, only to those plants less than thirty feet in height; and we know many trees the tops of which are three or more, even ten, times the height of a column of water supported against a Torricellian vacuum by the pressure of the air. Can the plant multiply this pressure?

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[34] Dixon, H. H., *loc. cit.*, pp. 95–99, 116–138, 203, 210.

[35] See Copeland, E. B., The Rise of the Transpiration Stream; an Historical and Critical Discussion. *Bot. Gazette,* 34, 1902; and Ueber das Saftsteigen. *Jahrb. f. wiss. Bot.,* 56, 1915.

This drives us back to capillarity, which depends upon the composition and form of the container as well as the surface tensions developed in the liquid itself under the influence of its container. The container being the ducts and tracheids of wood, opposing water movements by the attractions, adhesions, and imbibitions previously mentioned (pages 151–152), we cannot look for aid in this quarter. As to the menisci of the liquid itself, they also fail to furnish us with the requisite energy.

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[36] Le Chatelier, H., *Sur le mécanisme de la prise du plâtre.* Contes Rendus, Paris, 96, p. 617, 1883.

We know that evaporation at the top will concentrate the cell solution, the cell sap of the cells losing water to the intercellular spaces on which they border in leaves, etc. This concentration of cell sap will induce, if possible, an osmotic stream into the evaporating cells bordering the intercellular spaces, a stream of water which must be supplied from and by the ducts and tracheids. This implies negative pressure, or suction, of greater or less intensity, in the ducts and tracheids, a pull or traction on the columns of water therein which tends to break the columns just as the weight of the atmosphere tends to push them together. What then is the tensile strength, the coherence, of a column of water? Obviously this question may not be involved in the supply of water to the leaves of plants shorter than the limit of atmospheric pressure: but equally obviously it is inescapable in plants more than thirty feet tall, unless capillarity, or the pumping action of living cells should be proved to be adequate, and, as we have seen, they do not seem to be. That water has tensile strength is a matter of common observation, whatever may be said of the almost universal lack of attention given to this property of the most important "necessary of life." The measurement of the tensile strength of water shows that it is very considerable, and Dixon's measurements of cell sap[37] indicate that it at least exceeds 100 atmospheres. We see, then, that a column of water may be pushed up by a pressure of one atmosphere, but it will not break if it can be pulled up by many times that force. Is there any evidence that it is so pulled?

We know that the pressure in the vascular tissues of plants varies very widely, from the congestion familiar enough in the bleedings, weepings and runnings which occur when trees, etc., are wounded or "tapped" in the spring, to the suction which will forcibly draw water into similarly wounded or "tapped" plants in midsummer. The "root pressure" or sap pressure, so familiar a phenomenon in north temperate regions where deciduous perennials presently put out fresh foliage after the frosts of winter, has been claimed as the means of lifting water through the stems. However, the fact that, when the expanded leaves are losing most water and need it most, there is negative pressure or suction in the stems, would indicate the inadequacy, indeed the non-existence, of "root pressure" at such times. Root pressure, or sap pressure, can develop only when intake of water exceeds outgo, whether outgo be by photosynthetic combination of water with carbon dioxide, by secretion (see pages 166–176), or by evaporation. Such conditions can prevail for other land plants than those living in swamps and close to bodies of fresh water, still or flowing, only at intervals. The bald cypress (*Taxodium distichum*) of the southern swamps, for example, and the maples bordering streams, have an unlimited source of water at all times of the day and night. By maintaining the water gradient (pages 33–38) through their metabolic activities these trees *may* maintain root pressure throughout the season, the more readily because the humidity limits their losses of water: but do they?[38] At all events most land plants cannot do so, and some other explanation of the ascent of sap must be sought. Indeed why, in the presence of actual suction in the stems of land plants, one should entertain an hypothesis requiring the opposite, namely pressure, it is possible to understand only on the other hypothesis that reason does not control reason!

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[37] Dixon, H. H., *loc. cit.*, pp. 101 *et seq.*

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[38] There would seem to be a very promising field for study of sap ascent offered by trees living where there is always an ample water supply, as well as by those plants of dry and "physiologically dry" habitats. The last, so called by Schimper (39) owing to their salt or other deleterious ingredients, require other studies than have been made by the observational ecologists.

The tensile strength, or cohesion, of water having been demonstrated, the existence also of pressures or suctions respectively at different times and seasons, it remains to show what, if anything, can develop and maintain these forces and so apply them to columnar masses of water that these will move from under ground to the topmost leafy twig of the tallest tree. Assuming that Dixon is correct in estimating the requisite force as double the number of foot-pounds or calories indicated by the height of the tree, the force required to raise one cubic foot of water to the topmost leaf 100 feet above ground would be 200 foot-pounds or 155,600 calories. When one reduces this to grams, or to molecules, the proportion of the force to the mass of water to be moved is seen to be, after all, not so great. One must, however, realize that it will take more force to lift a solution than pure water, and hence at times when the sap is loaded — as in maples, grapes, etc., in spring — which are precisely the times of root or sap pressure, additional force may well operate to advantage.[40]

The amount of energy required to lift one gram (1 cc.) of water is .00234 cal. per meter. Many times this amount of energy exists, or is developed or absorbed, in the living cells of the leaves. Thus respiration (see pages 184–204) and evaporation liberate or develop much energy in the protoplasm and in the wet walls respectively, and much energy is absorbed during the hours of daylight, not all of which is employed in photosynthesis and in raising the temperature of the leaf. Respiration releases much energy in every living cell through-

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[39] Schimper, A. F. W., transl. by Fisher, W. R., *Plant Geography on the Basis of Physiology*. Oxford, 1903.

[40] As we shall see subsequently (pp. 168–173) the difference in weight between maple sap, for example, and pure water is, however, very slight, for at the most there are only 3.4 per cent of sugar in the sap.

out the plant. This amount is greatly in excess of what is used, as is indicated by the amounts liberated as heat (page 202). There is, therefore, no lack of energy released or absorbed in the plant. But is it applicable, and how is it applied to this particular task? This last question cannot be answered at the present time, although we may make ingenious guesses, and wish for further studies to bring the facts to light.

Both the rate at which water moves through the vascular tissues and also the rate at which it is given off by the plant have been the subject of repeated measurement. It is obvious that various factors of the environment affect both of these, and many studies of the external conditions influencing sap-flow and transpiration are reported in the extensive literature of the subject. The great handbook on the subject is the one by Burgerstein,[41] the completion and publication of which have been greatly hampered by war. Certain aspects of the subject have been studied with especial fruitfulness by investigators connected, temporarily, or otherwise, with the Department of Botanical Research of the Carnegie Institution of Washington. At the Desert Botanical Laboratory, Tucson, Arizona, and in many other stations where other conditions offered opportunity for comparable results, the rates of sap flow, of absorption and of loss of water, the "evaporating power of the air" (*i.e.*, the effects of its humidity, temperature, and movement), cell-sap concentration, the form and position of the root systems, and the anatomical structure of the parts of plants of the desert, the tropical "rain-forest" and of regions intermediate, have been the objects of study by MacDougal, Livingston, Harris, Cannon, Shreve, Pulling and many others, whose results are in the Publications of the Carnegie Institution of Washington. The establishment of a botanical laboratory in a desert region, in which the relatively few plants constitute a peculiar and striking flora, instead of being as unwise as has sometimes been charged, has given especial opportunity to study the relations of animals as well as plants to light, heat, water (liquid and vapor), and the various sorts of soil. Some of the fruits of this study we have already seen (page 71), others we shall see subsequently (see pages 311–313 on effects of light on vegetation and reproduction), and still others are contributions to the subject now in hand.

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[41] Burgerstein, A., *Die Transpiration der Pflanzen.* Jena, 1904, 1920.

Attempts have been made to measure the rate of movement of water through the vascular tissues by direct observation and by means of so-called potometers: and the determination by weighing of the loss of water from a potted plant, or from a cutting, throws a certain amount of light upon the rate of movement through the plant. But all of these methods are faulty as well as inadequate. The first method, of direct observation through microscope, lens, or unaided eye, can be applied only when dissolved coloring matters are introduced in the stream. Even a small wound is injurious, as indicated by the behavior of animals, and by the resulting fever temperature, as recorded by Richards and others:[42] but the shock to a living organ or organism produced by amputation may well cause the amputated limb or branch to behave unnaturally. Furthermore, there is no proof that the foreign substance, however innocuous chemically the pigment may be, may not be injurious for mechanical or other reasons, inducing irritations which may cause acceleration, or precipitations which may cause retardation, of the water current. It is nevertheless interesting to observe, for example, the more or less rapid rise of an aqueous eosin solution through the vascular bundles of translucent stems (*Tropœolum, Impatiens,* etc.), flowers which are white or other than red, or of leaves. In fact, such movement of colored solutions is used by commercial florists and other persons for the production of colored blooms, such as green carnations, pink chrysanthemums, etc.; and with the production in this country, or elsewhere, of inexpensive harmless dyes there is no reason why such monstrosities should not become more numerous. The conversion, for example, of white chrysanthemums into heads colored to satisfy the taste of the partisans of rival colleges at a football game is quite possible!

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[42] Richards, H. M., The Respiration of Wounded Plants. *Annals of Botany*, 10, 1896. Peirce, G. J., The Liberation of Heat in Respiration. *Bot. Gazette*, 53, 1912.

Amputated leaves, branches, and even stems may be inserted, air tight, into glass tubes the other end of which is of such size and position as to permit the measurement of the quantity and the rate of water movement from the source through the cut end and out into the air. These instruments, known as potometers, are of many forms, as may be seen in the laboratory manuals of plant physiology; [43] but they all suffer from obvious physical defects and, whenever a cut plant is inserted, they reveal the behavior of a part necessarily more or less morbid if not moribund. If one could transfer uninjured a whole wheat or other plant from a water culture into a potometer tube filled with a solution of the same composition, concentration, and temperature one would then be able to read off the results with much more confidence and satisfaction.

The methods thus indicated have, in spite of these defects, yielded results which show that water does move through the body of the plant at a sufficient rate to account for the great loss, as water vapor, in the course of a season. They do not throw light on the means of moving this great quantity of water. They show that, as we should expect, the rate varies not only with the condition of the plant but also with certain factors of its environment, notably with the temperature, the illumination, the humidity of the air, and the rate of movement of the air. Of the various devices which have been developed for measuring the water given off into the air, for measuring the ability of the air to take up water vapor, the porous-cup atmometer, as devised and developed by Livingston,[44] has proved most informing and satisfactory. Wet and dry bulb thermometers, and the hair and other hygrometers, while indicating with more or less accuracy the humidity of the air, may be made to give entirely misleading readings either by keeping them, as plants rarely are, free from drafts or, on the other hand, in wind. Thus, though there may actually be 60% humidity a plant will obviously lose water much more rapidly and in much larger volume in a breeze or a gale than in still air. A wet and dry bulb thermometer in a breeze would indicate not the humidity but the rate of evaporation and the consequent cooling under this condition. The porous-cup atmometer, on the contrary, is designed to indicate the actual amounts, rates, etc. of water uptake by the air, amounts, rates, etc. which will vary with the circumstances. As is well-known, this atmometer consists of unglazed porous cups of clay of standard size, form, and porosity, made for the purpose.[45] These, filled with *pure* distilled water, and connected by suitable glass tubing with suitable reservoirs from which the water can escape only through the surface of the inverted porous-clay cups, constitute exceedingly interesting indicators of the up-take of water by the air. By means of weighings at long or short intervals, or by means of actual measurements of the decreasing volumes of water in the reservoirs, the daily, hourly, or other loss of water can be determined. It is obvious that from a clean (*i.e.*, undusty, ungreasy, unsalted) surface the loss of water vapor need not be the same as from a leaf surface of equal area. Nevertheless, the limit of capacity of the air to take up water is indicated by such an atmometer. The loss by any given plant will be some fraction of this, a fraction directly indicating the ability of the plant to hold the water which it has absorbed and contains. The windy air under a cloudless sky moving over a wheat field on one of the "dry farms" of the semi-arid west has a great capacity for taking up water, as human thirst under these conditions indicates; but the growing or ripening wheat nevertheless holds its water, as water and water vapor, within its cells and in its intercellular spaces respectively, so long as the plants are able to absorb sufficient amounts from the soil. Wilting sets in when this last condition is not maintained.

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[43] For example, Ganong, W. F., *A Laboratory Course in Plant Physiology,* second or later edition. New York, 1908 or later.

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[44] Livingston, B. E., Atmometry and the Porous-cup Atmometer. *Plant World,* 18, 1915.

[45] The standardized cups may be obtained through the Laboratory of Plant Physiology, Johns Hopkins University, Baltimore, Maryland.

In an earlier chapter (pages 19–41) we have seen that, by reason of the contact of the cell sap of the root-hairs with the soil water, osmotic absorption of water takes place through the water-permeable walls of the root-hairs. The capacity of the plant to take up water is dependent upon the concentration of its cell-sap and the force with which the water is held on the surface of the soil particles, an attraction which, as we have also seen, is very great (pages 35–38) owing to the composition and physical condition of the soil. It has been thought that the water-holding and water-supplying powers of soils might be measured by osmometers[46] and by porous-clay cups or "points."[47] The results by both of these ingenious methods are interesting, informing, but by no means quantitative; for it is obvious that a plant will be able, by metabolic, as well as purely mechanical means, to maintain and even increase if need be, the concentration of the cell-sap in its root-hairs, whereas, in the usual osmometer, and certainly in the porous clay "point," which differs from a porous clay cup in being a pointed cone and in being used dry, the absorbing power will be progressively reduced from the maximum in the first instant of the experiment until the end. The absorbing power may be great in the first second, in the sixtieth it must necessarily be much less, and the rate of absorption will continue rapidly to decline until it affords no indication whatever of the "water-supplying power of the soil," for this will change, if at all, only unfavorably, in relation to the instrument designed to measure it, and to the plant.

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[46] Pulling, H. E., and Livingston, B. E., The Water-supplying Power of the Soil as Indicated by Osmometers. *Carnegie Inst.* (Washington) *Pub.*, 204, 1915.

[47] Livingston, B. E., and Koketsu, R., The Water-supplying Power of the Soil as Related to the Wilting of Plants. *Soil Science*, 9, 1920.

It may once more be remarked, in this connection also, that while one frankly recognizes and gratefully acknowledges the value of physical appliances in the study of physiological phenomena, there is an essential difference between them and those self-operating, self-regulating mechanisms which one also recognizes as living things. While the "water-supplying power" of soil in relation to porous clay "points" may be and will be indicated by their skillful use, the "water supplying power" of a soil will be small or great, as pointed out by Livingston and Koketsu,[48] according to the plant attempting to grow in it. Furthermore, the plant will vary its absorbing power, as we have seen (pages 000–000), according to its need, regulating the density of the cell sap of its root-hairs by its own metabolic activities. Again the experiments of Livingston and Koketsu fail to show any difference in the "water-supplying power" of "sand, loam, and humus" and "various mixtures of these" in relation to porous clay "points." This result is surprising, being quite contrary to general observation; for one sees different plants of the same species behaving, in respect to moisture as well as other factors of their environment, in different ways according to the soil and the quantities of moisture which it contains. The authors claim for this paper only the merits of a new contribution to science, not those of a finished product; but while one may welcome such attempts one should question whether they are based on sound or misleading conceptions. It may well be doubted whether an attempt in this form to treat the dynamics of the soil is just or justified. We must, as previously indicated (pages 125–131), consider the soil as a complex, with its corresponding forces as well as matters. But the expression "water-*supplying power*" implies a capacity on the part of the soil which must be the same, under the same conditions, to all sorts of things, lifeless and living. On the other hand, the water-*absorbing power* varies with the thing, lifeless or living. Thus the "water supplying power" of a blot of ink on a page of writing is a fixed quantity, no matter what the subject of the writing or the kind of paper; but the absorbing power of blotters and other objects which may be applied to the blot differs greatly. The physical and chemical nature of the soil, the humidity, temperature, and other qualities of the air, and the kind of plant, are the factors the resultant of which is the growing, thriving, or suffering organism. Under the same conditions one species will thrive, another die, depending upon the capacities of the organism rather than of the environment.

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[48] Livingston and Koketsu, *loc. cit.*

Turgor and Sap-Pressure

If, for any reason, absorption of water by a cell is more rapid than its use and loss, there will develop a pressure outward on the cell-wall. This pressure will vary with the ratio between intake of water and its use or loss. It will give to the cell and its walls a certain tenseness which is called *turgor* or *turgidity*. The importance of this in maintaining the form of cells, tissues, and organs without rigid walls is as great as it is evident. The shrivelling of an apple in dry air is due to the loss of water, the consequent decrease in pressure upon the walls of its cells, the loss in turgor, the more or less pronounced collapse of the cells. It is this loss of turgor which is the physical cause of the visible features of the familiar phenomenon of wilting, although wilting may, in its advanced stages, include even more than loss of water from living cells; for what may be recognized as extreme wilting may be the bending of purely mechanical tissue, made up of the walls of cells no longer living, under a changed and unbalanced load (see pages 239–241). The form, for example, of a cell of the alga *Spirogyra* is maintained by its turgor. It will quickly collapse when water is withdrawn either by evaporation or by immersion in a solution of greater density than its cell-sap. The former is a process repeatedly occurring in nature, when the streams or pools with *Spirogyra* growing in them dry up. The latter is a process occurring in nature only by accident, or deliberately produced in the laboratory. It is called *plasmolysis*. Plasmolysis has been used by De Vries and many others (see pages 34–38) to determine the density of cell-sap. Its opposite, *plasmoptysis*, consisting in exposing a cell to an aqueous solution of less density than the cell-sap, increases its turgor, because the cell absorbs water. The cells of organisms living in brines can be made to swell to a fatal degree by immersion in fresh or distilled water.[49] Even pollen grains, the walls of which are much more rigid than the walls of many other kinds of cells, may be made to burst in this way, the breaks in many cases occurring through the openings in the thick strong outer coat of the grains, the inner coat failing to withstand the strain in one or more of its unsupported parts.

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[49] Peirce, G. J., The Behavior of certain Micro-organisms in Brine. *The Salton Sea*, Carnegie Institution of Washington, No. 193, 1914.

If, instead of the *Spirogyra* cell or filament considered above, we imagine a slender, erect structure made up of many elongated cells attached end to end and the lines or rows of cells bound together by common walls, we shall have a structure in which the turgor of its component cells will produce mechanical effects some of which may be visible in the position or changed position of the mass. Thus we may have tissue tensions, due to turgor, or originating as turgor in living cells though persisting in many instances as strains, tensions, or compressions in tissues consisting only of the walls of once living cells. A dandelion stalk or a rose on its stem is such a mass, consisting of living epidermal and cortical cells, of lifeless ducts, tracheids, and other conducting and mechanical elements, and traces of pith around or in the center. They may be erect and carry the weight of the bloom at the top. On the other hand, a wilted dandelion stalk will not be erect or carry erect the head of flowers at the top, nor will a wilted rose do other than droop. Determinations of turgor and of tissue tensions will show that these are so *coördinated* in the fresh stalks as to give them their strength, elasticity, and erect position; and that the drooping of the head and of the stalk in wilting is due to decreasing and uncoördinated turgor of the living cells.

Changes in position of parts or organs in plants, as well as in animals, are often due to changes in turgor. Thus we see twigs, rapidly growing, or the buds opening on a spring day, or flexed seedlings as they come up out of the ground, becoming erect as the turgor of their cortical and other living cells increases.

The turgor, turgidity, turgescence of a cell or tissue or organ may be the means of exerting great mechanical pressure. Thus the pressure of the soil upon roots, while sufficient to cause their collapse if they die, is resisted by living roots however slender and delicate. Continued growth of roots may result in the applications of force sufficient to press apart blocks of stone or to raise stretches of pavement.

If the turgor increase beyond the holding power of the cell-walls the pressure may be relieved before the breaking or bursting point is reached by water escaping through the walls. Differences in permeability, mechanical strength, and perhaps other features of the wall (form, pressure from adjoining cells, etc.) account for these differences in behavior. The passage of liquid water, squeezed out through the wall, may occur on the surface of the plant or into the ducts, tracheids, and intercellular spaces. In consequence of high turgescence, wounds in the form of cracks may result, or tissue hypertrophies showing themselves as eruptions (intumescences), or water exudations through or between special cells (" water stomata," water pores, or hydathodes). Bleeding or weeping may also take place through wounds made by accident or design. These are extraordinarily diverse results of a common cause, as the following discussion will show.

If one grow seedlings of the ordinary grains in damp soil in the usually dry air of the laboratory, covering some of the dishes with bell glasses and leaving the rest exposed, the seedlings under the bell glasses will have drops of water, " dew," on or near their tips, although their fellows in the open air of the room may not. The reason is that, from soil equally wet, seedlings of the same age will absorb practically equal quantities of water through their roots, but will lose much less into the damp air confined under the bell glasses. In these circumstances the amount of water in the seedlings under the bell glasses will exceed the holding power of the cell walls and water will be squeezed out through the weakest places. Among these weak places are the tips of the leaves. This squeezing out of water has been called *guttation*. It commonly occurs at night, at times also in the day, on lawns and in other places where grasses and other herbaceous or even shrubby plants grow close together in damp soil over which cool air of high humidity lies nearly or quite motionless. It forms "dew"; for much of what we call dew is not such in the physicist's sense of "moisture from the atmosphere," precipitated when the temperature falls. Instead, the dew on the grass is generally moisture from the soil through the plants; it is in a sense physiological dew rather than physical dew.

In many plants the water, squeezed out generally from leaves, escapes not merely through cracks as in grasses, but through pores or water stomata, openings in the epidermis bounded by definitely and regularly arranged cells, as in the common garden nasturtium (*Tropæolum majus*), and from gland-like structures called *hydathodes* by Haberlandt and duly described by him,[50] as in scarlet runner bean (*Phaseolus multiflorus*) and other plants. Haberlandt concludes from the experiment of painting hydathodes with an alcoholic solution of corrosive sublimate, which kills the cells, that they are active glands, finding that water ceases to escape from hydathodes so treated, though others not so treated on the same leaf continue to be active. "An increased flow of water will be found to take place from the uninjured hydathodes." Haberlandt's conclusion is open to this objection, namely, that corrosive sublimate, as is well known, acting not only as a killing agent but also fixing or coagulating or precipitating the protoplasm or its constituents, greatly reduces the permeabilities of the cell membranes. If, therefore, there are uninjured hydathodes on the same leaf, the hydrostatic pressure which might be insufficient to force liquid through the increased resistance of poisoned cells would drive a correspondingly larger amount through the unchanged ones. Hydathodes may be glands, but as we see, Haberlandt's experiment does not prove it.

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[50] Haberlandt, G., transl. by M. Drummond, *Physiological Plant Anatomy*, pp. 487, *et seq.*

In the spring of the year, in the northern parts of North America, maple and other trees, and grape and other vines, exhibit in peculiar degree a phenomenon variously called bleeding and weeping. In maple the phenomenon is utilized on the commercial scale as the source of a highly prized syrup and sugar. The fame of the maple syrup and sugar of Vermont has tempted producers in other northern states to adopt the name; and the demand for maple syrup and sugar, even before the special food stringencies consequent upon the Great War, has kept the price high and made the maintenance of quality difficult. The operation of the Pure Food and Drugs Act, requiring on every package a declaration of its contents, while illuminating as to the composition of what was formerly sold as maple syrup and sugar, and tending to prevent dishonest adulteration, does not tend to increase the supply of maple products. It is entirely proper to put on the market substances designed to imitate maple products, if they are honestly declared; but it is very desirable, in the circumstances, to increase the supply which, if anything, is decreasing as sugar-maple trees and groves fall or are felled with increasing population. Owing to peculiar sensitiveness to seasonal conditions, the quantity of syrup and sugar produced by maple trees varies considerably from year to year; because of the short time during which the sap flows it is limited to a very few weeks in early spring; and because of the slow growth of the trees it is not a crop which can be grown within a small fraction of a man's life-time. For this last reason little planting is deliberately undertaken. In fact the largest fraction of the maple products comes from "wild" trees, the value of which was emphasized during the time when this country sacrificed itself to meet the shortage of sugar in Europe and later was sacrificed to meet a pretended sugar shortage invented by the cupidity of certain members of the sugar trade. With the gradual filling up of this country, and the decreasing frequency of transfer of ownership, there should be increasing planting for future, as distinguished from immediate returns. We are accustomed to forest planting, the fruits of which will not be realized by the generation that plants: but except in the parts of the country longest settled, like New England, New York and Pennsylvania, forest planting is mainly a government undertaking. But if an owner of suitable land can look forward to continued ownership of his land by his family or other congenial heirs, he may well consider planting a "sugar orchard," "grove," or "bush" as a private investment promising profit as well as public usefulness.

The conditions which give rise to the commercially useful "run of sap" on the sugar maple are those of guttation as previously described, namely an excess of water absorption over water loss. This is due to the combination of circumstances arising each spring in a belt running across the northern part of this continent. These circumstances and their results have naturally been most profitably studied in the maple sugar producing states. These studies constitute one of the important American contributions to botanical science, but even so, the literature of the subject is still quite limited.[51]

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[51] See Bryan and Collaborators, Maple sugar: Composition, Methods of Analysis, Effect of Environment. U. S. Dept. Agric. *Bull.* 466, Washington, 1917. Merwin and Lyon, Sap Pressure in Birch. *Bot. Gazette,* 48, 1909, *et seq.* Wiegand, K. M., Pressure and Flow of Sap in Maple. *Amer. Naturalist,* 40, 1906. Jones and others, in *Bulletin* 103, Vermont Agric. Exp. Sta., 1903, and in earlier Bulletins there enumerated, where also the literature is cited with useful fullness. This admirable series of studies is a fine example of American thoroughness!

The conditions of maple sap flow are these. In soil soaked with rain or sodden with melted snow which, as a blanket, has tended to keep the ground comparatively warm, the roots early resume their growth and develop hairs through which water may be absorbed. At the same time the lengthening days and increasing warmth of the sunshine raise the temperature in the trunks of the trees sufficiently to cause digestion of reserve foods, the conversion of starch into sugar in the places of storage, the migration of sugar from these places and the consequent spread of osmotic pressures through the body of a tree which make absorption of considerable quantities of water inevitable. Meantime the losses of water by evaporation from leafless limbs and branches can be only a small fraction of what will take place as soon as the buds open and the leaves unfold. Under these conditions there will be no fixing of water in photosynthesis. Hence circumstances both above and below ground combine to produce a condition of sap-pressure, a pressure of sap containing greater or less quantities of food, sugar, in the case of maple trees, in sufficient amount,[52] along with other flavoring substances, to make the concentration of the sap by evaporation commercially profitable. The pressure is sufficient to cause a flow of sap through the wounds deliberately made in "tapping" the trees. This outflowing sap is the saccharine solution expressed from the highly turgescent living cells into the elements of the wood along which it moves in the direction of least resistance, under the conditions of "sugaring off" through the holes bored in "tapping" the trees.

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[52] Analyses of sugar maple sap show, according to Bryan (*loc. cit.*), that such a solution contains not only sugar (2–7%) and water but a great variety of salts and other substances. These accumulate in the bottom of the evaporating pans in sugaring off as a collection of "dirt," the reason for the existence of which is generally not at all clear to the "sugar farmer" or the interested spectator.

In unwounded maple trees in spring-time, the direction of least resistance of sap-flow would be from the roots toward the tips of stem and branches, whence the name "root pressure." It is evident, however, from the discussion on page 155 as well as immediately above, that "root pressure" may develop whenever turgor exceeds the holding power of the cell walls and sap is forced out of living cells into the air-filled parts of the plant. Thus sap pressure, as it is properly called, may develop in amputated branches,[53] in joints of dahlia stalks,[54] and in any other parts in which water absorption exceeds water loss or use. The measurement of these pressures by manometers or other means is incomplete because the instruments indicate only the *net* pressures in considerable parts of the plant body. Within these parts the pressures may range both above and below the net or mean. The pressures, as recorded in the literature, may be indicated by the following quotations from the series of studies by L. R. Jones and collaborators at the Vermont Agricultural Experiment Station.[55]

Self-recording pressure gauges on two trees showed these conditions:

1	2
–2 lbs. (negative pressure or suction) at 9:30 A.M.	at 9:30 0.0 lbs.
12.5 " " " " " " 11:00 A.M.	at 12:00 10.0 lbs.
20.0 " " " " " " 12:00 M.	at 4–6:00 18.0 lbs.
15.0 " " " " " " 8:30 P.M.	at 7:A.M.–7.0 lbs.
–25.0 " " " " " before 10:00 P.M.	

Slowly declining and so remaining till morning, then rising till more than –5.0 lbs. about 6:30 A.M. then abruptly rising.

These figures indicate that there is an intimate connection between them and the daily rise and fall in the temperature of the air. There are, of course, modifications of this relation as the season advances, and also from season to season. In this range in pressure, the physical result of differences in temperature is at least equalled by the physiological result; for obviously secretion, digestion, and the other activities of living cells containing stored and other foods will vary with the temperature, they will absorb and expel water at corresponding rates, and hence they will regulate the sap pressure accordingly.

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[53] Pitra, A., Versuche ü. d. Druckkraft d. Stammorgane b. d. Erscheinungen d. Blutens u. Thränens d. Pflanzen. *Jahrb. f. w. Bot.*, 11, 1878.

[54] Kremers, E., Experimental Osmosis with a Living Membrane. *Science,* N.S. 48, 1918.

[55] *Bulletin* 103, 1903, pp. 70, 73.

Turning to the question of quantities involved in maple sap flow, Jones and his collaborators indicate that the sap ranges in richness from tree to tree from about 2% to about 7% of sugar. This range is due to age, size, exposure and other circumstances. In all probability too, individual variation in respect to sugar content of sap will equal what is known of milk and butter fat yields in cows, sugar and starch content in corn, etc., as recorded by the students of variation, and plant and animal breeding.[56] Five quarts may be "considered a fair average daily run for a tree" and "three pounds (of commercial maple sugar) is looked upon as a good yield, one which is often exceeded, but much more often not equalled, owing to seasonal conditions. Three pounds represents but about 9% of the total sugar content of the small tree, and it probably rarely represents more than 4% of the sugar present in a good sized tree."[57] One's fears as to the seriousness of this drain upon the resources of the tree are calmed by these students who state that, under ordinary conditions, such an amount can be spared without detriment, whatever may be said of the results of a cold and cloudy summer, of defoliation by frost or voracious insects, or of other interferences with food manufacture and storage during the season following "sugaring off."

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[56] Babcock, E. B., and Clausen, R. E., *Genetics in Relation to Agriculture*. New York, 1918.

[57] Jones, et alii., *loc. cit.*, p. 139.

The foregoing discussion has indicated the means by which water, with a load of organic and inorganic solutes, may pass out of the body of a plant through wounds, water stomata, and hydathodes. We should now consider the relation of the movement of water and other substances to other glands than those conspicuously concerned with the secretion of water. Such glands are either superficial, as for example the hairs on the surface of the common garden geraniums (*Pelargonium zonale*, etc.) which give the familiar fragrance, or subepidermal, as in the peel of oranges and similar fruits, or still deeper in the tissues, as the resin, tannin, rubber, and other reservoirs of coniferous and other trees, and of shrubs and other plants. It must frankly be admitted that knowledge of the physiological processes involved in the formation of the substances characterizing the various sorts of glands is mortifyingly disproportionate to their importance in the comfort, and even security, of human beings. While chemists and, to a certain extent agriculturists, have prosecuted their investigations of these products, botanists have, for the most part, ignored the producing plants beyond putting them in due position in classification and describing the curiosities of their anatomy.[58] Under stress of war or other necessity there may be spasmodic search for substitutes ("Ersatzmittel") for the accustomed raw or other materials; [59] but man has not yet, in the persons of botanists, made any adequate study of the physiological processes on which the satisfaction of his food and other requirements entirely depends.

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[58] For a very instructive summary discussion of the anatomy of glandular structures of many kinds see Drummond's translation of Haberlandt's *Physiological Plant Anatomy*, pp. 502, *et seq.*

[59] As for example Hall, H. M., and Goodspeed, T. H., A Rubber Plant Survey of Western North America. *Univ. of California Pub. in Botany*, 7, 1919.

Many of the substances characterizing such secretions or excretions being insoluble in water, their presence can be accounted for only on the supposition that, by oxidation or other change on the spot, they are formed from dissolved substances either made there or reaching there by dialysis. Thus the starch grains in the latex of many plants are undoubtedly formed in the laticiferous vessels from sugars made elsewhere but dialyzing into them. Such a conception is natural and easy, for we know that the storage of starch occurs by precisely this means elsewhere (see pages 16, 17, 170); but how can we conceive the continued secretion of sugar in nectaries, sugar beets, etc.? We must invoke (see pages 29 ff.) the hypothesis of changing permeabilities of the cell membranes; but even this does not completely indicate the physical and chemical means of accomplishing the end. In a nectary, whether within a flower or below it (extra nuptial), there are thin-walled cells directly bordering upon and forming the secretion. In sugar-beet "concentric zones composed alternately of xylem and phloem, the latter constituting the bulk of the storage tissue" of the root, accumulate sugar which necessarily reaches them in solution. In both instances it is imaginable that the sugar (saccharose) does not enter the secreting cell as such, but comes to it by dialysis in some other form. If this be the case, the transformation of the immigrant into saccharose within the cells of sugar-beet or outside on the surface of the glandular cells of nectaries, would result in no accumulation of sugar unless the cell-walls were impermeable to sugar. Obviously if a cell wall is impermeable to sugar outside, it should be equally impermeable within. Hence, if the cell wall bounding a nectary, or the cell wall surrounding a sugar-beet cell, be so impermeable to sugar as to prevent its return into the cell or its movement from it respectively, then it must be equally a bar to its movement in the opposite direction. Under the hypothesis of changing permeabilities we get no further; for if the cell wall be at any time permeable, must we not conceive its permeability as equal in opposite directions across it? In this case sugar would move in both directions, the rates depending, as elsewhere, upon relative concentrations and tending to establish a balance.

Another possibility must be considered in this connection. Nectar contains, besides sugar and water, various proportions of a number of other substances,[60] such as gum, other sugars than saccharose, and nitrogenous compounds. Similarly the cells of sugar-beets contain more than sugar. We can imagine that one or more of these substances may have an affinity for sugar and so hold it against osmotic pressure. Such an idea is not attractive. however, at the present stage of knowledge and ignorance.

We come back, therefore, to the hypothesis that the saccharose of nectar secreted by glandular cells on the surface of plants, and of sugar-beet sap stored in cells in roots, becomes saccharose in the place where it accumulates, reaching that spot in the form of some other compound (some other sugar?) and held in place by a cell wall impermeable to it. We know that the walls of sugar-storing cells of sugar-beets are impermeable to the cane-sugar.[61] What is the evidence of other substances entering the storage cells and being transformed there?

The movement of water into these sugar-secreting organs, whether superficial or internal, was shown many years ago by

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[60] See Haberlandt's *Physiological Plant Anatomy*, p. 508.

[61] Sachs, J. von, *Lectures on the Physiology of Plants*. Trans. by Ward, H. M. Oxford, 1887.

Wilson[62] to follow the usual course, the presence of dissolved sugar being the cause of water absorption by the nectar and by the sugar beet cells.

The formation of resin is explained, but with very incomplete knowledge of actualities, on the basis of water soluble substances passing through the thin-walled glandular cells lining the walls of resin reservoirs and undergoing, either in or on the walls, or in the cavity of the reservoirs, such transformation as forms the resin.

The formation of mucilages, gums, and the other substances, soluble and insoluble, secreted by plants and constituting the characteristic materials for which they are cultivated or collected for use in the arts, medicine, and the other ways of human life, is equally obscure and equally attractive to the student whether of pure or applied science.

In this same connection, as indicated above (page 166), the development of those peculiar eruptions called intumescences should be described. These sometimes present the appearance of pustules or tumors, or suggest galls. They are the outward evidence of edema, a condition in which the cells and tissues become overcharged with water because of reduced transpiration and continued absorption with no such means as guttation (see page 167) for excreting the excess of water. Thus, on bringing flats of seedlings of *Eucalyptus globulus*, which had grown in a lath-house, into the moist air of a greenhouse, I was greatly interested to see them presently break into an eruption which extended from the bark-covered bases of the little trees to all but the youngest leaves. The eruption became infected in certain instances with mold fungi, but most of the trees promptly recovered when the air of the greenhouse became less humid. In some cases the eruption follows mechanical or chemical injury. In any instance, however, the balance between evaporation (transpiration) and absorption is changed, resulting in increased water content. It is claimed that the increased capacity for hydration is due to changes in " the cell colloids resulting from acids produced by oxidation." Further research alone will determine the value of this explanation.[63]

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[62] Wilson, W. P., The Cause of the Excretion of Water on the Surface of Nectaries. *Unters. a. d. Bot. Inst. z. Tübingen.* Leipzig, 1881–85.

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[63] Wolf, F. A., Intumescences, with and without Mechanical Injury and Cause of Their Development. *Journ. Agric. Research,* 13, 1918.

VII

METABOLISM

In the preceding chapters the various processes connected with the intake and movements of raw materials, and the manufacture of food have been discussed. All of these processes have involved energy. Energy has been expended in doing work or energy has been stored, fixed, transformed from kinetic to potential. Thus the sources and supply of material and energy for living plants, and hence of animals also, have been discussed. We have seen that material and energy are accumulated in the bodies of plants as the products of synthetic chemical changes.

Material and energy are released, made available, and used, by means of destructive or analytic chemical changes. These analytic changes take place within living cells just as do photosynthesis and the other processes concerned in food manufacture. They are therefore, in this sense, vital phenomena; but examination shows them to be of the same sorts as other chemical reactions. The intra-cellular reactions releasing material and energy for construction and operation of the living organism are also chemical reactions of the same sorts as occur outside. Material is employed in maintenance, offsetting wear and tear; in growth, which constitutes permanent increase in size, and in operation, which requires release of energy. The reactions resulting in offsetting wear and tear take place when and where they are needed; they take place at rates varying with circumstances. Those reactions concerned in growth vary also, circumstances influencing the occurrence of growth as to time, place, and speed. The kind of growth is also influenced by circumstances (the environment), but within limits corresponding, as in laboratory chemistry, with the substances concerned. Hence any study of growth so inevitably involves the study of circumstances also that we may well consider it under the heads of the various factors of the environment, and their influence on living things (pages 223–350).

The release of energy to do work, as required by the living organism, is also regulated by circumstances, as we shall presently see. In every living thing energy changes occur from the beginning to the end of its existence. These energy changes, the accompaniment of chemical change, go on continuously throughout life. It is only in the figurative language of Scripture — "except a corn of wheat fall into the earth and die"[1] — or in purely theoretical discussion — "if a man die shall he live again?"[2] that the question ever arises whether, if material and energetic changes actually stop, they can ever be started again and life continue.

The experiments of Becquerel,[3] in which he employed liquid hydrogen to produce a temperature of −250° C., as previously used by Thistleton-Dyer[4] and Dewar, show that ordinary air-dry seeds, of the sorts experimented upon, are not only able to withstand such extreme cold, but that, in such cold, they are also in an almost perfect vacuum, and all chemical action is so greatly reduced that in fact, if not in theory, there appears to be none. Yet after such exposure these authors found normal germinations, indicating not only that the very greatly reduced vital processes of oxidation, *et cetera,* increased their rate quite normally, but also that the consequences of such metabolic processes, growth and development, proceeded as if nothing unusual had occurred.

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[1] John xii., 24.

[2] Job xiv., 14.

[3] Becquerel, P., Recherches sur la vie latente des graines. *Ann. d. Sci. Nat., Botanique,* 9 Sér. 5, 1907. Recherches experimentales sur la vie latente des spores Mucorinées et des Ascomycètes. *Comptes rendus de l'Acad. des Sci.,* Paris, 1910.

[4] Thistleton-Dyer, W. T., On the Influence of the Temperature of Liquid Hydrogen on the Germinative Powers of Seeds. *Annals of Botany,* 13, 1899.

Under the conditions of these experiments the air-dry seeds contained at least 10 per cent of water. What is the condition of this water in air-dry seeds? That it is held by considerable forces is indicated by the difficulty with which it is removed; it can be drawn off only slowly and incompletely by concentrated sulphuric acid, anhydrous phosphoric acid, and other drying agents in desiccators; and it can be driven off only by heat. A drying oven sufficiently cool to escape hurting the protoplasm is not able to drive off all the water. One may attempt to distinguish between the water of composition, which cannot be driven off without chemical destruction, and the water of constitution which, forming a part of the colloidal system called living protoplasm, cannot be driven off without physical ruin. Only the latter can be thought of as being drawn off in a desiccator or driven off in a drying oven. If it is completely removed by either process the living colloidal system will be a wreck. Can it be restored merely by the return of the water? We can readily conceive that the self-operating mechanism will cease to act when its mechanism becomes defective; or when the conditions of temperature, etc., make operation impossible. But we are not compelled to conclude that resumption of activity, the revival of metabolic processes, must be coincident with the restoration of water or the elevation of temperature.

Cold storage, preserving by the addition of sugar, drying, and other methods employed on the domestic or commercial scale for conserving foods, owe their value and effectiveness not to any devitalizing process nor to any which completely checks or prevents metabolism in the organisms or tissues concerned, but rather to the slowing of one or all of these processes in all the organisms which may be accidentally associated. Thus, in apples, meat, etc., in cold storage, metabolic processes are very slow, also in the bacteria and fungi on their surfaces. None of these methods is satisfactory for prolonged preservation, however, unless it may be complete drying, because the results of slow metabolism, consisting in broken-down tissues and in accumulated by-products, impair or destroy the value of the stored material. In all of these cases we have what Becquerel properly calls retarded, not suspended, animation.

On the other hand, high temperatures insufficient to decompose the substances concerned in metabolic changes in living organisms, nevertheless profoundly affect or stop metabolism. Thus, what is known as *heat rigor* may be produced by temperatures which a chemist would regard as moderate, but at which movement of protoplasm, growth, and other visible vital phenomena will cease. These may be reestablished if the temperature fall, but a continued even small rise in temperature beyond the point at which rigor occurs may produce death. Furthermore, experience shows that while a given temperature may be endured for a short time, with or without heat rigor, the same temperature will produce death if maintained too long. Thus while we may have a fatal temperature which instantly produces death to organisms exposed to it, temperatures considerably lower may be equally fatal if prolonged.

The effect of temperatures not immediately fatal is sometimes seen on the great scale out-of-doors. Thus during the winter 1921–1922 in western middle California cold prevailed for an unusual length of time. The data, as reported by E. S.

Nichols, Meteorologist at the U. S. Weather Bureau Station, San Jose, for the month of January, 1922, are as follows:

Highest temperature, on the 25th, 62° F.
Lowest " " " 21st, 23° F.
Minimum temperatures, 7th to 16th inclusive, between 33° and 30° F.
Minimum temperatures, 19th to 24th inclusive, between 25° and 27° F.
Minimum temperatures, 25th to 31st inclusive, between 36° and 35° F.
Average daily deficiency of the month as compared with normal, –5.27° F.
The lowest temperature in 16 years, 22° F.

Damage to tender plants was very great, not only as recorded by the growers of citrus fruits but also as observed on other plants by many other persons. Plants which hitherto had withstood low temperatures on single cold nights were greatly hurt or killed by the long succession of cold nights. The visible effects of the cold were, especially, the change in color of normally evergreen leaves, which looked as if they had been burned, — *e.g.*, *Eucalyptus globulus, Quercus agrifolia* — and the splitting of the bark of such cultivated shrubs as *Eugenia*.

How are these effects to be explained? Temperatures not high enough or low enough to destroy compounds or to prevent chemical action are found to produce heat rigor or death on the one hand, or cold rigor and death on the other. The results may be accounted for provisionally, in the absence of definite knowledge, on the hypothesis that the physical conditions and the rates of chemical change which permit living are so affected in individual particulars that that balance which constitutes normal metabolism and makes life possible is temporarily or permanently destroyed. In the multitude of chemical reactions of which the living cell and the living body are the seat, the rates are not the same nor influenced to the same degree by the prevailing temperature. Hence we may conceive one or another of these reactions to be so accelerated or retarded that it does not coördinate properly with the others going on simultaneously. The result is a slowing or clogging of the mechanism, interrupted metabolism, rigor, or death. Further discussion of the relation of temperature may be deferred to the chapter on Irritability (pages 329–333). The above discussion, however, indicates that the prevailing temperature, as a factor of the environment (see pages 225 ff.), profoundly affects other vital processes than those concerned in the phenomena called irritable.

The chemical changes taking place in living cells and living organisms are collectively called *metabolism.* This definition is so broad that it implicitly includes all of the constructive reactions resulting in the manufacture of foods. Animal physiologists, however, having no opportunity to deal with the fundamental synthetic reactions of carbohydrate synthesis and only to a limited extent with protein synthesis, are in the habit of applying the term metabolism to the *use* of food by the living organism. The older terms *anabolism* and *catabolism,* applied to constructive and destructive metabolism respectively, have not come into general use; and plant physiologists may well follow the example of the animal physiologists in using the general and inclusive term *metabolism* as practically synonymous with catabolism.

Metabolism, destructive metabolism, or catabolism results in changes in energy and material. In certain metabolic processes the energy changes appear to be important, in others the material changes. For this, presumably, the reasons are to be found in the history of the science rather than in the facts themselves. But it is evident that no chemical changes can take place without accompanying and corresponding energy changes. Hence the foods, made as we have seen in the foregoing pages, can be used either as sources of energy, as fuel, or by additional expenditure of energy, as building material. Furthermore, it is evident from the foregoing (pages 55–72) that the foods, made by the application of energy, will release a certain amount of energy when broken down to the simple compounds (raw materials) out of which they were built. The processes which most evidently release energy are those in which oxidation of foods takes place.

It should be noted at once, however, to be discussed later (pages 213–222), that, in addition to the oxidation of foods there is, in some organisms, the oxidation of certain substances (H, H_2S, S) which cannot be considered anything more than fuels, from which energy is derived for operation. In the great majority of both animals and plants carbon compounds which are foods are oxidized. These constitute the main source of energy for operation. Oxidative metabolism is, then, almost invariably, thought of as the oxidation of carbon compounds, but we must also consider the oxidation of other substances than the compounds of carbon which are utilized by plants as sources of energy.

The vital processes of living organisms are intra-cellular, involving changes in both matter and energy. The process of photosynthesis, accomplished within living cells containing chlorophyll, stores energy. Energy is released by the oxidation of the stored products of photosynthesis. When this oxidation takes place within living cells energy is released therein.

Intra-Cellular Oxidation

Whereas the "objects" or "purposes" of such processes as photosynthesis are perfectly evident, food being the principal and indeed the obviously needed product, there is no such desirable obviousness about those intra-cellular oxidations which botanists have commonly called respiration. We may follow the example of some of the animal physiologists,[5] who call them *internal respiration* as distinguished from the mechanical processes accomplishing the supply and the drainage of the cells. Plants have no propelling or conveying mechanisms, they do not alternately inhale and exhale, they have no heart, lungs, or gills, no arteries, veins, or capillaries. Their respiration is entirely intra-cellular, entirely metabolic. In all living organisms the products are material and energetic. The relations of these products to the needs of living organisms as we understand them have not led us to any satisfying conceptions as to the reasons for such internal changes. The oxidizable compounds laboriously constructed are automatically destroyed with a release of energy apparently greatly in excess of the requirements. Not more than twenty per cent. of the calculated number of calories are applied to do work, the remainder are exhaled or radiated, at all events not applied, and hence lost. The material products are similarly excessive, if the living machine is in reality correspondingly inefficient. We may guess that the principal use of the energy liberated by intra-cellular oxidation and immediately converted into work is in carrying on those syntheses of food not energized directly by the light absorbed by the chlorophyll pigments. In fact, unless the syntheses of amino-acids, proteins and nucleo-proteins from sugar and the nitrates, sulphates, and phosphates, are restricted to those cells receiving a sufficient amount of suitable light, the energy for these operations must be transferred to the cells making the complex organic compounds containing nitrogen, sulphur, phosphorus, and magnesium. The transmission of energy, whether inside or outside the living cell or living body, is generally in the form of currents (wind, water, electricity), or in the form of fuel. The fuels are combustible oxidizable solids or liquids; some of these are soluble in water and hence are movable through any permeable septa. Under the laws of diffusion previously examined (pages 31–41), the moving of the sources of energy to the spots (or cells) where they are to be used, molecule by molecule, is conceivable. But while all this may constitute a clear picture in our minds, the amount of fuel supplied and used seems excessive in proportion to the synthetic or other work done.

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[5] Bayliss, W. M., *l. c.*, p. 600.

In plants muscular action resulting in movements does not exist. There are motile plants and plant parts, but they are small, and other mechanisms much simpler in structure than muscles accomplish the movements. They are duly energized, but they are few and relatively inconspicuous. On the whole, we do not need, in studying plants, to account for the supply of any considerable quantity of energy. But plants continue to accumulate potential energy in their stores of food (tubers, bulbs, seeds), and to release kinetic energy by oxidation within their cells, in amount apparently quite in excess of their own needs as synthetic and otherwise energy-consuming organisms (see pages 156–7).

The three main products of carbon metabolism are carbon dioxide gas, water, and energy, very commonly in the form of heat. These are the principal products of the oxidation of carbohydrates, and of many other non-nitrogenous carbon compounds both outside and inside the body. Though they may be and are produced within living cells, they do not remain there, nor may they accumulate there. In animals the respiratory mechanism is as necessarily concerned with the removal of the products of intracellular oxidation as it is with the supply of oxygen. The respiratory mechanism of the higher warm-blooded animal, and of the fish, for example, removes heat as well as carbon dioxide. In the case of the land animal it also removes larger or smaller proportions of the water produced in oxidation. In plants the products of intracellular oxidation make their ways to the world outside the tissues of the body along the same courses taken by the oxygen. These are the paths of gaseous diffusion and of movement of dissolved substances (pages 19–41). A limit to the size and compactness of a mass of living cells is, therefore, set by the rate at which the compounds and the products of intracellular oxidations can move by diffusion and dialysis. Hence what has previously been said of stomata and intercellular spaces (see pages 51–55), in discussing the supply of CO_2 to chlorophyll-containing tissues, applies equally to the stomata as "breathing pores" and to the lenticels and intercellular spaces as paths of gaseous exchange. Thus oxygen and CO_2 will be taken in through open stomata; but they will also pass through the cuticula and the walls of epidermal cells, thus providing entrance and exit for the two substances most intimately concerned. The rates at which the two substances will enter and leave a given cell, tissue, or organism will depend, as we have seen, upon the partial pressures of the respective substances inside and outside the living cell and upon the permeabilities of the membranes to be traversed. A decrease in permeability may conceivably interfere to a dangerous extent with the intake of oxygen or the outgo of carbon dioxide in an active living cell. Change in permeability may therefore affect respiration as well as other metabolic processes.[6]

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[6] Winterstein, H., *Die Narkose*. Berlin, 1919. Osterhout, W. J. V., A Theory of Injury and Recovery. *Journ. Gen. Physiol.*, 1921. Palladin, V. I., transl. by Livingston, B. E., *Plant Physiology*, 2nd ed., 1922.

The release of energy in plant cells is ordinarily conceived to be accomplished by the oxidation of sugar, the oxygen coming from the air. The chemical reaction is usually written thus:

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$$

but just as there is the utmost difficulty in discovering the stages in which the opposite reaction, that of photosynthesis (pages 55–72), takes place, so plant physiologists are far from agreement as to the course of this reaction accomplished outside the living organism only at temperatures far above those which prevail within them or which living organisms can withstand. A succession of theories of increasing difficulty and complexity has marked the continued study of the subject. Beginning with such simple reflections as "the kindling hypothesis," that the smaller the particles of combustible (oxidizable) substance the more intimate the mixture of it with oxygen and the lower the temperature of ignition (oxidation), theory has now summoned enzyms and other catalyzers,[7] electro-chemistry,[8] stereo-chemistry,[9] and finally radiology,[10] as the means of accomplishing or at least of explaining an action which all living organisms have presumably always carried on.

We naturally think of the oxidation of sugar, whether inside the body or in the laboratory, as consisting in the oxidation of carbon, but the structural formulæ of the hexose sugars indicate that neither the hydrogen nor the carbon is saturated, although the proportional formulæ, as usually written, suggest the complete saturation of the hydrogen with oxygen. Presumably, therefore, both hydrogen and carbon ions can unite with oxygen, if the conditions within the cell are suitable. Light on the question is thrown by Dakin[11] who, discussing the subject of physiological oxidations, refers especially to the discovery by Hopkins[12] of a substance which oxidizes spontaneously at the temperature and under the other conditions of the live cell. Hopkins names this "glutathione," and claims that it is generally present in living cells. If Hopkins and Dakin are correct, there must be considerable revision of the conceptions of the processes of respiration, intramolecular respiration (see page 204), and oxidation held by many persons, and probably it is not yet possible to know the facts.

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[7] Green, J. Reynolds, *Fermentation,* 2nd ed. Cambridge, England, 1901. Oppenheimer, Carl, *Die Fermente und ihre Wirkungen,* 5te Aufl. Leipzig, 1924.

[8] Nathansohn, A., Ueber kapillarelektrische Vorgänge in der lebenden Zelle. *Kolloidchemische Beihefte,* 11–12, 1919–20.

[9] Warburg, O., Physikalische Chemie der Zellatmung. *Biochemische Zeitschrift,* 119, 1921.

[10] Becking, L. B., *Radiation and Vital Phenomena.* Utrecht, 1921.

In the first place, while CO_2 and H_2O are common end-products of carbon metabolism, they are not always formed, the oxidation being, for one reason or another, incomplete. This is true, for example, in the well known case of hemp. In intramolecular respiration of peas, CO_2 and H_2O, though formed, are not even the main products. In certain fermentations (see pages 204–212) the breakdown of the carbohydrates is incomplete and alcohol, or other unsaturated compound, is formed more abundantly than the theoretical end-products. Some, at least, of these reactions can take place in the absence of free oxygen, in which case one has imagined oxygen ions moving from hydrogen to carbon, or *vice versa*, in either case releasing a certain amount of energy. While a part of the process obviously consists in the transfer of oxygen from one element to another, energy being released, Dakin[13] has shown that the "oxidation" of an aldehyd to formic acid, carbon monoxide and carbon dioxide, can take place where there is no free oxygen. Instead of *oxidation* there is actual dehydrogenation. The result is an increased *proportion* of oxygen and the liberation of energy. Oxidation, therefore, does not necessarily consist in the addition of oxygen to the material in question, although it does involve the union of oxygen ions with others; but it does often consist in the removal (or withdrawal) of hydrogen and the liberation of a saturated hydrogen compound. This idea makes it easier to conceive what takes place, for example, in the fermentation of bread dough. In the usual bread dough the proportion of free oxygen in the sticky mass is necessarily small. Nevertheless, CO_2 and H_2O are formed when the yeast has had time to multiply sufficiently in warmth and moisture (pages 207–209). In this case there is dehydrogenation. To be sure, the result is the same, but the means are different.

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[11] Dakin, H. D., Physiological Oxidation. *Physiol. Reviews*, 1, 394+, 1921.

[12] Hopkins, F. G., An Autoxidizable Constituent of the Cell. *Biochemical Journ.*, 15, 286+, 1921.

Common experience informs us that in many plant cells there are substances which take on color on exposure to air. The change in color is due to oxidation, which may take place normally. Palladin[14] gave the name of "respiration chromogens" to these compounds. He considered them to be not only of almost universal occurrence in plant cells, but to play an almost indispensable part in the oxidations taking place within them. Presumably many bacterial pigments, formed only on exposure to air, are of the same sort. The connection of these pigments with oxidation for the release of energy in

[13] *Loc. cit.*, p. 399+.

[14] Palladin, V. I., Livingston, B. E., *Plant Physiology*, 2nd ed., pp. 222–3, 1922. Synergin, das Prochromogen des Athmungsfermentes der Weizenkeime. *Biochem. Zeitschr.*, 27, 1910.

the living cell, as described by Palladin, corresponds to the rôle attributed by Dakin and Hopkins (see page 189) to "glutathione," namely that, in solution in the cell, sugar splits into CO_2 and hydrogen, the hydrogen going to a "prochromogen," possibly a glucoside, which thereby becomes a chromogen. This, in the presence of oxygen, becomes brown or red or even a purple. Under the conditions ordinarily prevailing in the living cell, however, the chromogen thus oxidized splits off water, becoming a prochromogen once more. Thus the production of both water and carbon dioxide are accounted for. Palladin's theory also successfully employs the oxidizing enzyms, the oxidases, which are known to activate oxygen at the temperature prevailing in living cells. The action of these may appropriately be discussed in connection with certain fermentations (pages 204 *et seq.*).

We may now proceed to examine the phenomena which plant physiologists have called respiration. In these phenomena in which oxygen and non-nitrogenous carbon compounds are concerned, and the final products of which are carbon dioxide, water, and energy in the form of heat, most attention has been given to the production of carbon dioxide and least to the production of water,[15] although neither is invariably formed. On the other hand energy is always released, some of which necessarily escapes as heat. Respiration may be studied quantitatively by determining its material or its energetic products. Thus we may have a given weight of germinating peas from which certain determined quantities of CO_2 and H_2O are produced, and a certain amount of heat is liberated. If the dry weight of the peas before germination is compared with their dry weight say forty-eight hours after they have been put to soak in water (to start germination) it will be found that they have lost weight. If, furthermore, the experiment is so conducted as to enable one to determine the amounts of substance absorbed by the germinating peas, it will be found that they will absorb about weight for weight of water, that is, that 100 grams dry peas will absorb about 100 cc. distilled water; and that the volume of O_2 taken in almost exactly equals that of the CO_2 given out. In other words, the absorption of enough water makes normal activity possible, and under ordinary conditions, oxygen consumption equals CO_2 production. Analysis, both microscopic and chemical, shows that the great change in the composition of the germinating peas is in their carbohydrate content, starch and sugar being consumed. If now we set up an experiment at ordinary temperature, in such manner that a constant stream of air, from which all trace of CO_2 has been removed, is drawn through a bottle containing germinating peas, it will be found that the air passing away from the peas contains CO_2. Various means have been employed for determining the amounts of CO_2 produced by the peas, as may be seen from the papers of Osterhout[16] and his associates, and the literature therein listed.

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[15] Babcock, S. M., Metabolic Water; Its Production and Rôle in Vital Phenomena. *Univ. of Wisconsin, Agric. Exp. Sta., Research Bull.* 22, 1912.

Similar methods applied to plants (and animals) or their parts in various stages of their development show that the consumption of oxygen varies with the circumstances, the activities, and the kind of organism. Thus it is found in plants, as in animals, that the activity of the organism as measured by its gas exchange, varies with age, size, and environment, and in ways characteristic of the species. The warmth ample for the bacteria of the North Sea would be insufficient for the corresponding species, for example, of the Red Sea: but it should be recognized at once that the influence of temperature upon respiration is, to a certain extent at least, indirect, that by limiting the other activities of the organism the temperature affects the processes releasing energy and ordinarily producing CO_2 and H_2O. This is familiar to the animal physiologist and the surgeon, who know that whatever chills the body unduly, whether it be the interference with respiration due to anæsthesia or the actual cooling of the body by excessive radiation, may produce death or at least pneumonia, or its equivalent, with their effects upon respiration. The statement may then be made that the optimum temperature for the organism is also the optimum for its respiration, and that if the temperature is above or below the optimum its respiration will correspond. In this respect respiration appears to differ from some of the other bodily functions, of which it is often said that they do have optimum temperatures, *i.e.*, temperatures at which these functions are most active. Thus we find that growth may be most rapid at a certain temperature. There is no question, for example, that hot nights favor rapid growth in corn; but though cool nights interfere with rapid growth in corn and many other plants, mere warmth or coolness at night will not alone determine whether the corn will grow fast or slowly, for humidity, fertility, and freedom from competition will profoundly affect it also. The reason for this is to be found in the principal product of respiration, — namely, energy.

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[16] Osterhout, W. J. V., and others, Comparative Studies on Respiration. *Amer. Journ. Physiol.*, vols. 1 to date. *Amer. Journ. Bot.*, 9. Apparatus for the Study of Photosynthesis and Respiration. *Bot. Gazette*, 68, 1919.

The means of measuring the energy yield in respiration, in both plants and animals, are as various as the means of determining the material products. While the material products may be generally and mainly CO_2 and H_2O, they are not necessarily so. The energetic products, on the other hand, are either chemical energy, which reveals itself as work done, or heat, the presence of which is ascertainable in the usual ways. The secondary importance of the material products is indicated by the fact that they are by no means always the same, and that while so much attention has been given to CO_2 where it is formed, little notice has been taken of the water generally found with it. The importance of all three — the CO_2, H_2O, and heat — may be illustrated by the condition of wheat or other grain or seed, for example, in storage, and potatoes, fruits, etc., in transit.

Wheat and other grains in the field contain water. If this water content be increased by the grain becoming wet, as sometimes happens in the shock in a season of summer showers, the grain may sprout at once. If the grain be threshed and transported or stored while still damp it may sprout, or mould or mildew. On the other hand, dry grain will bear transportation and storage without injury. Assuming that the dry grain has come uninjured through the various mechanical processes of threshing, etc.,[17] it may be kept indefinitely before being milled; but the water content of the grain, the temperature of its surroundings, the completeness with which the principal products of its metabolism (respiration) are removed, will all affect it as a source of food, to say nothing of its viability as seed.

Formerly the seeds used for experiment in my laboratory were kept in ground-stoppered bottles or jars. Finding that the seed frequently moulded or otherwise spoiled in glass, I sacrificed the convenience of the transparency in glass and now use tins which have either cap or compression lids. These exclude mice, but the covers need not be so tight as to prevent fairly free gas exchange. Thus an accumulation of moisture in the seed container may occur, but it is unnecessary. This moisture is what Babcock has called *metabolic water,*[18] for it is formed in the course of the oxidation of carbohydrate food by the living, though relatively inactive, seeds. Deterioration such as this, on the small laboratory scale, may take place on the gross commercial scale, and has been the subject of extensive studies in applied plant physiology. Thus Bailey and Gurjar[19] report their study of wheat in storage.

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[17] An assumption not justified by experience. Obviously the breaking or wounding of the grain greatly increases its exposure to infection, besides the irritation by the injury itself (see p. 203).

"Heating" and "curing" are generally due to metabolic changes recognized as connected with, if not constituting, respiration. "Heating" may be due to fermentation carried on by a foreign organism (mould fungi, bacteria, etc.); but ordinarily it, as well as "curing," is due to the destructive metabolism of the material itself. Grain may heat in the bin, elevator, or hold, and while the simultaneous activity of foreign organisms is by no means excluded,[20] the result is due in no small part to the more abundant organism, the grain itself. Thus it is shown that the rate of respiration in fully ripened sound wheat of low moisture content (12.50% or less) is low, but that it rapidly increases with increase or accumulation of moisture in the grain. This is indicated by the yield of CO_2, by the rise in temperature or the heat yield, as well as by the change in moisture content. "Haynes Bluestem" wheat containing

12.00% moisture produced 0.54 mgr. of CO_2 per 100 gr. of dry matter in 24 hours.
13.93% moisture produced .65 mgr. of CO_2 per 100 gr. of dry matter in 24 hours.
14.78% moisture produced .86 mgr. of CO_2 per 100 gr. of dry matter in 24 hours.

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[18] Babcock, S. M., *loc. cit.*

[19] Bailey, C. H., and Gurjar, A. M., Respiration of Stored Wheat. *Journ. Agric. Research,* 12, 685 +, 1918.

[20] See Darsie, Elliott and Peirce, *Bot. Gazette,* 58, 1914.

15.42% moisture produced 1.62 mgr. of CO_2 per 100 gr. of dry matter in 24 hours.

17.07% moisture produced 11.72 mgr. of CO_2 per 100 gr.

In other words, the metabolic activity of the grain, leading to germination or other spoiling, using the material for which the food stuff is harvested and stored, is directly proportional to the amount of moisture originally stored in the grain or absorbed or liberated by it. To preserve the grain for seed or food purposes its physiological activity must be kept as low as possible. This can be accomplished by drying, ventilating, and cooling.

Grain in transit is more subject to injury than is grain in storage, for it can be worked in the elevator or even in the bin as it cannot in car and cargo. Thus Duvel and Duval[21] show that with increase in moisture content of corn in transit in a freight car there is increasing loss in weight and in quality:

	Corn when loaded		*Loss in weight*		*Temperature when*	
Car	*Moisture*	*Weight*	*Pounds*	*Percent*	*Loaded*	*Unloaded*
1	16.7%	66.940	.120	.18%	58° F.	62°
2	17.4%	67.160	.180	.27%	54°	58½°
3	17.8%	65.920	.290	.44%	54°	82½°
4	18.6%	67.120	.320	.48%	52°	84°
5	19.8%	67.130	2.450	3.65%	58°	139½°

Baerner[22] gives corresponding figures for corn in ocean transit,

Corn when loaded		
Temperature	*Moisture*	*Temperature discharged*
33.33 F.	18.9%	37 — 132°F. = 84.75° average

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[21] Duvel, J. N. T., and Duval, Laurel, Shrinkage of Shelled Corn while in Cars in Transit. *Bull. U. S. Dept. Agri.*, 48, 1913. Bach, E. A., and Cotton, R. T., The Effect of Fumigation upon the Heating of Grain Caused by Insects. *Journ. Agric. Research*, 28, 1924.

[22] Baerner, E. G., Factors Influencing the Carrying Qualities of American Export Corn. *U. S. Dept. Agric. Bull.* 764, 1919.

and shows that, by keeping down the moisture content of the grain, its metabolic activity will be correspondingly low, no matter what its temperature at time of loading or during transit. Grain can be safely carried for long distances, or safely kept for a long time, so far as its food value is concerned; for unless the grain be sufficiently moist to enable it to be active, there will be only very slight chemical change, if any, in it. Germination and all other vital processes will be delayed or prevented.

On the other hand many food stuffs are stored or shipped while still alive and while necessarily containing large proportions of water. The fruits and root crops are examples of this sort. The art of cold storage, and of the cooling and pre-cooling of fruit cars and fruit steamers, has developed to check their metabolic activity and that of associated organisms (bacteria, fungi). The shipment of oranges and other citrus fruits, and of deciduous fruits, over long distances is possible only at low but moderate temperatures. Hence the practice of cooling the cars and contents before starting (pre-cooling) and of icing them in transit. The root crops, on the other hand, are much less tender and there is more danger from freezing temperatures in winter than there is of undue warmth in transit or storage. Nevertheless, as shown by Bartholomew,[23] potatoes may brown or blacken at the heart without infection of any kind if they become sufficiently warm from their own metabolism. Their food value, as well as their sale value, becomes correspondingly less.

The so-called "curing" of many fruits, in the course of which changes in color, sweetness, and other properties occur, is due to the metabolic activity of the living cells. These activities include the liberation of heat and of carbon dioxide, water, and other substances. But there are also included in the various forms of " processing " to which citrus and other fruits are subjected in commercial practice, as distinct from the simpler domestic methods, chemical changes, due to the action of one or another of the external agents applied to the fruit. Thus, while lemons may " cure " on the shelf or on the rack without other attention than care as to the temperature and humidity of the surrounding air, " sweating " and other means of modifying the color or flavor of fruit may be due to the action of gaseous substances liberated in the sweating house by the fuel employed to maintain the temperature. In the former instance the " curing " is the result of metabolism; in the latter, the " sweating " is an artificial chemical process to which the fruit is deliberately subjected by the producer. In both instances, however, changes which would produce similar appearances in the natural course of events are either put under control so that they may be hastened or delayed at will, or they are initiated under control, for commercial reasons. These practices in scientific horticulture are, therefore, applications of principles in plant physiology to economic problems.[24]

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[23] Bartholomew, E. T., A Pathological and Physiological Study of the Black Heart of Potato Tubers. *Centralbl. f. Bacteriologie*, 43, 1914. Also Bartholomew and Bennett in *Technical Publication* 14, *College of Agriculture, University of California.*

These considerations suggest questions as to why many seeds and spores do not germinate when the fruits ripen, but seem to require a " resting period " or time for " after ripening "; and also as to how long seeds, spores, and other " resting " protoplasts will retain their power to germinate. Gardeners' and seedsmen's practice is concerned with both of these questions also.

The difficulty of germinating certain hard-shelled seeds is due to anatomical causes. These can be overcome only by facilitating the entrance of water and oxygen. This may be accomplished by such mechanical and chemical means as will soften or thin the shells, filing, grinding them with abrasives, treating them with concentrated sulphuric acid, etc. But in many instances proof is still lacking as to the actual deterrent in other cases of delayed germination. Whether, when the fruit is ripe, the embryo is still so undeveloped in the seed as to require more time to complete itself,[25] or whether digestive enzyms or other substances must be formed in sufficient amounts before germination can take place, appears to vary in different plants.[26] Still other plants, as we shall see later (pages 299, 330), require special conditions of heat or cold, light or darkness, or specific chemical stimuli before their seeds will germinate.

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[24] Wright, R. C., Coloring Satsuma Oranges in Alabama. *U. S. Dept. Agric., Department Bulletin* 1159, 1923.

The longevity to which seeds, spores, etc., may attain varies not only with the conditions and with the species but appears in certain instances to have an anatomical basis. Thus, in general, seeds contained in hard or thick shells, as those of many *Leguminosæ*,[27] or in fruits which may remain unopened for years, as the cones of certain pines,[28] retain their germinating power much longer than most. Hemp seeds sprout best in the next growing season, and they cannot be successfully held over, under ordinary conditions of storage, for more than a year or two. The spores of many ferns, liverworts, mosses and algæ, have very restricted germination powers. This is without question closely connected with the ordinary experience of their respective species; but it is actually due, not to the usual succession of the seasons nor to inherited habits but to the lack or loss of material upon which one or another of the processes resulting in germination depends. Some spores and seeds, for example, lose their germinating power when dried; others will not germinate until after they have dried. The California buckeye (*Aesculus californica*) drops its large seeds or its one-seeded fruits at about the time when the first rains begin, late in October in this part of California, and the seeds sprout before they can dry out. They do not germinate well if dried. On the other hand, the spores of many of our liverworts do not germinate well till after they have dried. Between Becquerel's ten seeds of *Cassia bicapsularis* of which three germinated, although upwards of eighty-five years old, and the restricted germinating powers of many garden seeds, there are all gradations. It is obvious, however, that, other things being equal, fresh seeds will germinate better than older ones, and the buyer is absolutely dependent upon the integrity of the seedsman. As already indicated (page 194), the environment of semidormant organisms, such as plants in the seed or spore condition, and the other resting stages of algæ, liverworts, mosses, etc., will also have decided influence upon their ability to germinate.

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[25] Goebel, K., *Organographie der Pflanzen,* 2nd ed. Jena (p. 454, 1st ed.). (See also Molisch, Pflanzenphysiologie, 4te Aufl., p. 295.)

[26] Harrington, G. T., and Hite, B. C., After-ripening and Germination of Apple Seeds. *Journ. Agric. Research,* 23, 1923.

[27] Becquerel, P., Recherches sur la vie latente des graines. *Ann. Sci. Nat. Bot.* IX, 5, 1907. Ewart, A. J., On the Longevity of Seeds. *Proc. Roy. Soc.,* Victoria, 1908. Goss, W. L., The Vitality of Buried Seeds. *Journ. Agric. Research,* 29, 1924.

[28] Jepson, W. L., The Silva of Calfornia. *Memoirs of the University of California,* 2, 98, 104–5, 1910.

Sometimes it occurs in nature that fire or other devastating influence clears an area once occupied by forest or other plant cover, and that a new cover, different from the old, appears to spring up out of the ground. In cases of volcanic devastation this new cover is the product of spores, seeds, etc., blown and otherwise brought in; but in other cases, while such a process is not always excluded, neither is the germination of dormant seeds long hidden in the forest floor or under chapparal or herbage. One wonders as to the duration of the dormancy of these seeds suddenly called into activity, for laboratory experiments have not yet completely illuminated this phenomenon.

The measurement of metabolism in plants consists in the quantitative determination of the material or energetic products. The former [29] is the older and more usual way, the latter [30] perhaps the more significant. The determination of the quantities of CO_2, H_2O and of other substances produced is accomplished by the usual methods of chemistry. The determination of the quantities of energy released is accomplished by the use of calorimeters of various sorts. From the very large, elaborate, and defective calorimeter chambers of such size as to contain an ox [31] to those employed in testing small quantities of seeds or determining the heat yields of chemical reactions,[32] there are many varieties, the common principle of which is to minimize the loss of heat by insulation of one sort or another. Going no further back than the work of Bonnier [33] we find that felt, air, and water jackets were the main insulators employed in the older types of even the best apparatus. While such insulators employed in the forms of clothing, housing, etc., are satisfactory where considerable losses of heat are of slight importance, man's practice of using skins and furs in seasons and regions of extreme cold, and the feather covering of birds, teach us the inefficiency of our ordinary insulators. The double walled glassware invented by Sir James Dewar [34] for work on liquid air, etc., and apparently separately devised at about the same time by Rubner, now in general use under the name of thermos bottles, offer the most perfect heat insulation so far produced. This consists of double-walled glass vessels, the adjacent walls plated with silver, and the space between thoroughly evacuated. The glassware is obtainable in cylinder, flask, and other forms, the most available, though by all means the most uncertain as to quality, being the so-called thermos refills used in replacing the broken interior of the ordinary thermos bottles. By the use of thermometers, thermal couples and galvanometers, and the other methods of calorimetry,[35] the heats of chemical reactions, of the metabolic activities of animals, and of plants, can be determined. This has been done by several investigators with the results thus indicated.

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[29] Osterhout, W. J. V., A Method of Studying Respiration. *Journ. Gen. Physiology,* 1, 1918.

[30] Peirce, G. J., Liberation of Heat in Respiration. *Bot. Gazette,* 53, 1912, *et seq.* Doyer, L. C., Energie-Umsetzungen während der Keimung von Weizenkörnern. *Recueil d. trav. bot. Néerland.,* 12, 1915.

[31] Hagemann, O., Das Respirations-Kalorimeter in Bonn und einige Untersuchungen mit demselben bei zwei Rinden und einem Pferde. *Landw. Jahrbücher,* 41a, 1911.

[32] Molisch, H., Ueber die selbsterwärmung bei den Pflanzen. *Zeitschr. f. Bot.,* 6, 1914.

[33] Bonnier, G., Recherches sur la chaleur végétale. *Ann. Sci. Nat. Bot.* VII, 18, 1893.

Plant	*Air Temp.*	*Calorimeter Temp.*	*Time*	*Heat yield per hour per Kilo.*	*Author*
Wheat grains........		at° 0.0° C.	Beginn. Germin.	0 Cal.	Bonnier
		5.7°		180–360 "	"
		10.5°		720–900 "	"
		15.8°		2100–1920 "	"
Peas................		30.0°	4th day	513 "	Peirce
Wheat...............		30.0°	4th "	5600 "	Doyer
Dandelion heads.....	17°	56.6°	5th "		Molisch
Pine twigs & needles..	21.3°	27.1°	2nd "		"
Submersed water plant	20°	43.8°	" "		"
Leaves of Ailanthus...	20°	31.8°	" "		"

Such quantitative methods as above described, which may be employed for considerable times continuously, enable one to compare the activities not only of different species or individuals, but also the same species or individuals at different ages, and also to apply the results to the determination of the activity, and hence presumably the value, of different lots, for example, of seeds. Thus one may recognize that there is a "normal temperature" for peas just as there is for people, and that departure from this indicates debility or infection in both instances.[36] Infection may be superficial and unimportant, or it may be very serious, affecting the germinating power and the productiveness of the seed. Debility is commonly due to the seed being old. Germination tests indicate that heat yields give the same indication of the value of seeds. The thermos bottle test, however, is much the quicker.

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[34] Dewar, J., New Researches on Liquid Air. *Proc. Roy. Inst.*, London, 1896. Liquid Hydrogen. *Ann. Rep. Smithsonian Inst.*, Washington, 1901.

[35] Ostwald, W., Luther, R., *Hand- und Hilfsbuch zur Ausführung physicoschemischer Messungen.* Latest edition, Leipzig, ?. Findlay, Alex., *Practical Physical Chemistry*, 4th ed., London, etc., New York, 1923.

The above table explains, to a certain extent, the heating of grain in transit as previously discussed (pages 195–197). The heat-yields are due to oxidations, principally of carbohydrates in starchy seeds, of the fats and oils in oily seeds, of the proteins also in all seeds. Presumably these or corresponding processes go on in all living cells. Owing to the complexity of every living cell, to the great diversity of its contents, and to the number of chemical changes taking place simultaneously in it, the determination of the partial sources of the total sum of released and unused (lost) energy is at present impossible. Furthermore, these figures make it still harder to understand the great yields of energy in organisms which, because they are sedentary or sessile, do not require as much as their more active competitors. As Dixon has pointed out, however, the work done in lifting the great volumes of water absorbed and evaporated by trees implies the application of great quantities of energy (see pages 156–157). This energy must be liberated where it is needed, it cannot well be transmitted from part to part. The intracellular release of energy, by metabolic process, chiefly oxidation in the end, furnishes a great amount of energy always available, the unused portion of which readily escapes by radiation or otherwise.

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[36] Darsie, Elliott and Peirce, *loc. cit.* Peirce, G. J., Testing Seeds with a Thermometer. *The Scientific American Monthly*, 1920.

The processes previously discussed have been tacitly assumed to take place in the presence of the proportion of oxygen usual in the atmosphere. It is known, however, that whole animals[37] and whole plants[38] may, at times at least, continue to "breathe" even when insufficiently supplied with oxygen; and it may be guessed that many plant and animal cells in the deeper, more compact tissues of larger plants and animals lack oxygen in ordinary proportions either very generally or at least occasionally. In such cases, while more or less completely oxidized compounds may be formed — *e.g.*, CO_2 — incompletely oxidized compounds are also formed of which ethyl alcohol is one of the commonest. As previously indicated, the chemistry of this process is difficult as yet to understand. The phenomenon has been called *anaerobic* or *intramolecular respiration.* As the foregoing discussion suggests, the name may be misleading because it may imply more similarity to ordinary respiration than exists.

Fermentation

Presumably because, in certain instances, the substances acted upon and the end products are more or less the same, plant physiologists have regarded fermentation as essentially a form of the same phenomenon as that which they have called respiration, and which I have spoken of in the preceding pages as oxidative metabolism. Reflection shows, however, that while the substance acted upon may be the same, the end products include very different substances. Alcoholic fermentation by yeasts, for example, while taking place in starch and sugar preparations and while yielding CO_2 and H_2O and energy, also yields alcohol (C_2H_5OH), which is not a product of ordinary respiration in plants. It is formed, however, in certain instances of intramolecular respiration, of peas for example. Alcoholic and other fermentations are therefore commonly spoken of as connected with those processes termed respiration or intracellular respiration or oxidation by plant and animal physiologists. This is, I think, a misleading practice because (1) not all fermentations are oxidations, and (2) in all fermentations the metabolism of nutrition is quite as much involved as is metabolism for the release of energy. This latter phenomenon is the only one properly called respiration. In fact fermentation, involving digestive and other nutritive processes, might be discussed in the chapter on nutrition.

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[37] *E.g.*, frogs, leeches, etc. See Bayliss, *l. c.*, p. 611.

[38] *E.g.*, peas, as in the common laboratory experiment. Ganong, W. F., *A Laboratory Course in Plant Physiology*, 2nd. ed. New York, 1908.

When one thinks of all the fermentations that one knows about, one realizes that they are accomplished by living organisms, minute and peculiar. In many instances the tools or agents are known by which these organisms accomplish their characteristic chemical changes. In other instances neither the agent (enzym) nor the chemical change or product is known. The changes accomplished man may employ for his own benefit, or they may be inimical to him. What are generally recognized as fermentations, such as alcoholic, lactic, butyric, etc., do not differ essentially from decay, decomposition, putrefaction, and disease, each being characterized by products or processes peculiar to itself, though these are the results of the operation of the same principles. Thus the putrefaction of meat, characterized by offensive smells, the partial and odorous decay of codfish incidental to its drying for market, and the partial and faintly odorous decomposition of milk ingredients in the manufacture of cheese, result in the production of materials considered respectively as poisonous, innocuous if not universally approved as to flavor, and generally acceptable. Presumably typhoid bacteria also act on similar proteins in the human digestive tract. Furthermore, similar changes seem to go on in corresponding substances without the intervention of foreign, more or less invading, organisms, enzyms accomplishing autolytic as well as fermentative changes. Thus the American palate prefers beef "not too fresh," the Englishman wishes his mutton "high," and the German orders his venison in actual decay. The American's beef "not too fresh" has been acted upon by its own enzyms (autolysis); the Englishman's mutton has increased in tenderness and changed in flavor both autolytically and by the destructive action of bacteria; the German's venison has been softened and modified in flavor by autolysis and completed for cooking by the organisms of decay and putrefaction. Similar, though less familiar and obvious changes take place in plant tissues as the result of the action of enzyms formed by and within themselves. How much more than loss of water takes place in lumber allowed to dry slowly in the yard is not now known, although the inferiority of kiln-dried to air-dried lumber, and the differences in odor of these two sorts in certain instances, suggest that, even in wood, autolytic changes may well occur. Autolytic changes certainly occur, however, in plant tissues during drying after ripening, and in connection with germination. Some of these enzymatic processes are scarcely distinguishable from those designated as digestive. It is not necessary to trouble ourselves over these designations, however, if the essential likeness of the phenomena is recognized. The characteristics of fermentation may be the more plainly recognized if we consider specific examples.[39]

Alcoholic fermentation, because it is used in the raising of bread, the production of liquors, and the manufacture of ethyl alcohol for use in the arts, has long been an object of intent study. Whatever its sociological status may become, the production of alcohol must be very seriously considered as a source of liquid fuel, in case a substitute for petroleum products has to be found. The materials usually employed in alcoholic fermentation are the grains or flours of the highest food value. These contain carbohydrates, either directly fermentable themselves or easily convertible into fermentable substances (sugars). The list of possible sources of alcohol is, however, very much greater than the list of sources commonly used. With the increasing food requirements of growing populations, other than food substances must be used for the production of industrial alcohol. There are two great supplies of these not now utilized to any extent, the importance and value of which will become increasingly recognized, namely the vegetation of the humid tropics and the vegetation of the seas, from both of which fermentable materials may be inexpensively prepared and worked.

As implied above, the principal material products of alcoholic fermentation are CO_2 and ethyl alcohol (C_2H_5OH). In addition, fifty-seven calories are liberated per gram-molecule of sugar. The balance of the potential energy of the sugar (326 calories) may be liberated by the complete oxidation of the alcohol inside or outside a living body, or it may be liberated in part by such partial oxidation of the alcohol as occurs in acetic acid fermentation (125 calories, see page 210). But it goes without saying that while a high degree of accuracy in the determination of the course of a reaction and of its products, material and energetic, is possible under the controllable conditions of a laboratory, no such control and no such accuracy are possible in the study of living organisms themselves. Thus, while pure cultures and even pure strains of yeast may be employed to act on a pure starch or pure sugar in a suitable solution, the products will not be merely alcohol, CO_2, and heat. Part of the energy liberated will be used by the yeast cells, part of the material formed will consist of "by-products." These latter are of the utmost importance in bread and in wine making; for if they are of disagreeable taste or flavor, or if they are pleasant, the value of the domestic or commercial product will be influenced accordingly. The "bouquet" of wines is due to these by-products. The objectionable properties of "home brew" depend in part upon them.

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[39] See Green, J. Reynolds, *Fermentation,* 2nd. ed. Cambridge, England, 1901. Oppenheimer, C., *Die Fermente,* 5th. ed. Leipzig, 1924.

Yeast is the principal agent of alcoholic fermentation, but mucors and many other plants produce alcohol under suitable conditions. The yield of alcohol and of by-products by different species and strains of yeast, and of the mucors, etc., varies very considerably. Great care is therefore exercised by the more conscientious and intelligent producers of yeast and of alcohol to maintain the purity and activity of their yeasts. Contaminations by inferior strains or species of wild yeasts, by bacteria, and by moulds, all of which readily occur under domestic conditions and in carelessly conducted commercial establishments, while reducing the yield of ethyl alcohol, may increase the by-products to a dangerous degree. Among these must be mentioned the so called "fusel oils," other alcohols than ethyl, chiefly amyl, to the presence of which "moonshine" and other illegal liquors owe their poisonous and violently intoxicating properties.

In the common bread fermentation commercial yeast is mixed with water which is added to a mass of flour formed by grinding wheat (or other grain). This flour consists principally of starch and proteins. As there may be a deficiency of sugar at first, a small quantity of sugar is added to the dough to help the yeast to start. The yeast, at suitable temperature, multiplies rapidly in the dough and forms enzyms which act upon the substances concerned. Thus the starch in the dough is converted by a diastase or amylase, present in the flour but also formed by the yeast, into maltose. This is split by maltase, formed by the yeast, into glucose. The glucose is then acted upon by zymase with the result that CO_2 and alcohol are formed. Cane sugar, itself not fermentable by yeast, is advantageously added to the dough, for the invertase formed by the yeast will split it into fructose and glucose, the latter of which is immediately fermentable, as above. The reactions are indicated thus:

$$\begin{aligned} 2\ C_6H_{10}O_5 + \text{amylase in water} &= C_{12}H_{22}O_{11}\ \text{(maltose) dissolved} \\ C_{12}H_{22}O_{11} + \text{maltase in water} &= 2\ C_6H_{12}O_6\ \text{(glucose)} \\ C_6H_{12}O_6 + \text{zymase in water} &= 2\ CO_2 + 2C_2H_5OH\ \text{(alcohol)} \end{aligned}$$

Neither yeast nor any other organism forming alcohol can continue to do so indefinitely, even in sugar solution, unless adequately supplied with the other constituents of protoplasm. The ordinary nutrient solutions of yeast — bread dough, the must of grapes, and the mash of grains — contain phosphates and other mineral matters in due proportions. Thus we see that the production of alcohol and CO_2 by yeast cells involves the nutrition as well as the energetic metabolism of these organisms. For theoretical and practical studies of fermentation the reader is referred to the literature.[40]

In acetic fermentation, acetic acid or vinegar is made by the oxidation of dilute ethyl alcohol. The organisms ordinarily accomplishing this change are species of Bacterium which form an alcohol oxidizing enzym. This may be extracted from their cells by acetone[41] and, in cell-free solution, proved itself to be the active agent by bringing about the oxidation of alcohol to acetic acid. The manufacture of vinegar is an important commercial process depending, as we thus see, on the activity of certain living organisms which produce a catalyzer, the enzym which brings about the oxidation of ethyl alcohol at ordinary temperatures. The energy liberated is about 125 calories per gram-molecule. In the usual method of making vinegar the heat is immediately dissipated by radiation. Apparently the best temperature for the process is rather low (20–30° C). If the supply of alcohol fails, the organisms apparently complete the oxidation, breaking down the acetic acid to CO_2 and H_2O.

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[40] Harden, A, and Young, W. J., The Function of Phosphates in Alcoholic Fermentation. *Centralbl. f. Bakr.* II, 26, 1910. Hansen, E. C., late Director of the Carlberg Laboratory in Copenhagen, devoted to

The gaseous products of fermentation sooner or later escape, unless acted upon meantime. The solid or liquid products, being less motile, accumulate unless removed. The CO_2 of alcoholic fermentation ordinarily escapes, the alcohol accumulates. So also with acetic acid, and with the other products of fermentation. These ultimately check the process because they are harmful to the ferment organisms. In this respect the ferment organisms are like all others: beyond a certain point they are hurt by their own products. Yeasts may be made to produce under suitable conditions 14% of

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fermentation studies, and editor of its *Meddeledser,* in which valuable contributions are published. Schnegg, H., *Das mikroskopische Praktikum des Brauers,* 1 and 2. Stuttgart, 1921–22. Jörgensen, A. P. C., *Microorganisms and Fermentation.* Philadelphia, 1911. Lafar, F., Transl. by Salter, C. I. C., *Technical Mycology: the Utilization of Microörganisms in the Arts and Manufactures.* London, 1903–10.

[41] Buchner, A., and Gaunt, R., Ueber die Essiggährung. Liebig's *Ann. Chem. u. Pharm.,* 1906.

alcohol. Wines and liquors containing more are "fortified" by the addition of alcohol, or are made by distillation (whisky, brandy, etc.). Acetic bacteria can still be active in solutions containing up to 14% of free acid. The fungus *Citromyces* is said to be able to continue its production of citric acid from sugar until 20% of acid have accumulated.[42]

The subject of acid production has recently undergone partial investigation under the caption of hydrogen-ion changes.[43] While these are shown to be more or less specifically characteristic, the physiologist welcomes evidence that the phenomenon is not only studied exhaustively but is seen in its relation to the rest of the activities of the organisms concerned.

Many fermentations are useful to man. Among these are the ones resulting in the souring of milk, the production of the almost numberless varieties of sour milk drinks and of cheese, the coloring of butter, the curing of tobacco and the extraction of fiber. Most of these are described in detail in technical publications.[44] One may, however, make the distinction here, as based on the facts of tobacco curing and fiber extraction, that while these processes are catalytic, the active and perhaps the characteristic, specific enzyms may be produced, for example, by the tobacco leaves themselves rather than by the accompanying bacteria; and careful experimental reinvestigation of the practice of fiber extraction may well show that the usual process of retting is wasteful and unnecessary, at least under certain climatic conditions. Just as in the making of bread, beer, and wine, care and precision in operation have brought certainty in result, so the scientific study of other processes, carried on roughly since time immemorial, may be expected to improve the yield both in quality and quantity.

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[42] Wehmer, C., *Beiträge zur Kenntniss einheimischer Pilze*, 1, 1893.

[43] Weimer, J. L., and Harter, L.L., Hydrogen-ion Changes Induced by Species of Rhizopus and by Botrytis Cinerea. *Journ. Agric. Research*, 25, 1923.

[44] Lafar, *loc. cit.*

Disease in man, and in other organisms — including plants — is due in many instances to fermentations. These may be accomplished by enzyms produced by the organisms themselves, or by enzyms formed by invading organisms. While the details of these will be found described in the books on pathology, whether of plants or animals, these too must be recognized as physiological processes due to chemical change produced by catalytic action. The study, for example, of plant disease from this point of view is gratifyingly extending and defining the chemistry of disease, and facilitating the prevention and treatment of disease.

As indicated above (page 188) the majority of living organisms secure their required energy by oxidizing compounds of carbon. Whether such oxidations take place directly or indirectly, by the oxidation of the H or C ions of the compounds, the final result is the production of CO_2, H_2O and the liberation of energy. The energy values of such oxidations are indicated by the following figures.[45]

C.	amorphous to CO_2	96.9	Cal. per gram molecule
	diamond to CO_2	93.24	Cal. per gram molecule
	dextrose to $CO_2 + H_2O$	709.02	Cal. per gram molecule
	dextrose to alcohol	67.00	Cal. per gram molecule

The energy values of certain other materials may also be cited.

1 gram bread crumbs (carbohydrate and protein)	3984 calories
1 gram butter	7264 calories
1 gram wood charcoal (mainly carbon)	8080 calories
1 gram hydrogen	33881 calories

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[45] Ostwald, S., *Lehrbuch der allgemeinen Chemie*. Bd. 2, p. 92, *et seq*. 2nd ed. Leipzig, 1903.

Oxidation of Hydrogen

The enormous energy value of the oxidation of hydrogen, as formerly utilized in the oxy-hydrogen blow pipe with its application in projection lanterns, and at the present time in acetylene lighting and welding, make one wonder why carbon, with its relatively low energy yield, should be so nearly the universal fuel, at least on the earth and among its inhabitants.[46] Very few organisms appear to make any direct use of hydrogen, or of other hydrogen compounds than H_2S, as sources of energy, and very few persons other than Russians seem to have studied the phenomenon.[47]

Since hydrogen must be liberated in the breaking down of certain complex organic compounds there would be a considerable and an increasing amount of this gas in the atmosphere if it were not recombined as rapidly as it is liberated. As it is, the proportion of hydrogen in air is negligible and there is therefore, in Nature, a hydrogen "cycle," just as there are "cycles" through which all of the other constituent elements of living organisms pass. Thus, in soil and in water there are bacteria which oxidize H to H_2O. The yield in energy is obviously very high, the reduction in volume from two gases to one solid is very great, and while one commonly regards water as innocuous, yet a moment's reflection shows that, as the most nearly universal solvent known, and in almost every other way, it is a tremendous power in the world within and outside of all living things. So far, we know only bacteria, and of these only a very few species, which use the oxidation of hydrogen as the source of needed energy.

[46] See Henderson, L. J., *Fitness of the Environment.* New York, 1913.

[47] See "Autoreferat" of Niklewski, B. Ueber die Wasserstoffaktivierung durch Bakterien. *Centrallb. f. Bakteriologie,* Abth. 2, 40, 430, *et seq.,* 1914.

Oxidation of Sulphur

A very much larger number both of species and individuals among the bacteria oxidize hydrogen sulphide, H_2S, as a source of energy.[48] While these organisms have this particular capacity in common there is great diversity among them in other respects. Some live only in fresh water, others in salt, some precipitate only sulphur in their bodies, others ferrous sulphide in or upon them; some are colorless and hence absolutely dependent upon the products of other organisms for food (heterotrophic), others contain a pigment, bacteriopurpurin, which has been compared in its functions with chlorophyll,[49] in that the organisms possessing it can combine CO_2 and H_2O into food (autotrophic). While some of the sulphur bacteria, so-called, are capable of forming organic compounds for food, they ordinarily do not do so, but those living in water rich in organic matter absorb some of this organic matter as food. The majority of sulphur bacteria live in waters which owe their H_2S content to the decomposition of organic sulphur compounds by other bacteria, those of decay. These waters contain food as well as fuel for these organisms. In mineral springs containing H_2S the gas is presumably of inorganic origin, and it is accompanied only by raw materials out of which foods may be synthesized. We may clearly distinguish then — (1) living organisms deriving from their environment only the raw materials for the manufacture of food and fuel, (2) those which derive both fuel and food from their environment, and (3) those which derive their fuel from their environment but make their food from raw materials. The first category includes all self-supporting green plants, the second all animals and the parasitic and saprophytic plants, while the third comprises the relatively small number of plants which must make their food but, like some of the sulphur bacteria, some of the hydrogen bacteria, some of the nitrogen, and the iron bacteria, oxidize substances which they directly absorb from outside themselves.

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[48] Winogradsky, S., Ueber Schwefelbakterien. *Bot. Zeitung,* 1887.

[49] Molisch, H., *Die Purpurbakterien.* Jena, 1907. Becking, L. B., The Source of Energy of the Sulphur Bacteria. *Proc. Soc. Exp. Biol. and Medecine,* 22, 1924.

We are now concerned with the metabolism of those organisms which oxidize sulphur and sulphur compounds for the release of energy. In the sulphur bacteria of fresh and salt water, or of mineral springs containing H_2S, there may be ions of H_2S, S, HS, and there may be oxidation of any or all, according to circumstances. At all events the matter is not clear at the moment. The direct oxidation of H_2S liberates about 60 calories per gram-molecule, and the sulphur accumulates in the cells of the bacteria themselves in the form of rhombic or monoclinic crystals or in amorphous condition.[50] The sulphur particles constitute a fuel reserve, drawn upon only when the supply of H_2S becomes inadequate. The oxidation of rhombic sulphur to SO_2 yields about 71 calories per gram-molecule.[51] In the case of the colorless sulphur bacteria the energy thus liberated may be used not only for the operation of the living machine, whatever this loose expression may for the moment imply, but also for the synthesis of organic food from the raw materials present in the waters in which they live.[52] On the other hand, the so-called red sulphur bacteria, while deriving their operating energy from the oxidation of H_2S and S, may make their own food from the raw materials of their surroundings, utilizing for that purpose the light energy absorbed by their pigment.

The relation of the sulphur bacteria to ferrous and perhaps other sulphides may be of economic as well as theoretical importance at times in water supplies and in connection with planking or other wood, concrete, and masonry in water and mud. Indeed there may also be geological significance in this relation. In mud and in waters containing organic compounds of sulphur, with iron also present, the liberation of H_2S by the bacteria of decay may result in the precipitation of black sulphide of iron as well as the supply of fuel to sulphur bacteria. The insoluble ferrous sulphide may, however, be used as a source of sulphur, which is thereupon oxidized as a source of energy. The SO_2 thus formed may unite with water, become still further oxidized to sulphuric acid, and neutralized to salts by the iron and by the alkaline elements also released in the destructive metabolism of soil and mud bacteria. The course of the reactions may be represented thus:

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[50] Baas-Becking, L. G. M., Studies on the sulphur bacteria *Ann. Botany*, 39, 1925.

[51] Ostwald, W., *loc. cit.*

[52] Winogradsky, S., *loc. cit.*

$$FeS + O_2 + \text{aq.} = SO_2 + Fe(OH)_3 = H_2SO_4 + Fe(OH)_3$$
$$H_2SO_4 + \text{iron or alkaline elements} = \text{sulphates}$$

The result is the return to water and soil of soluble sulphates, the sole compounds of sulphur of which the independent green plants of land and water can make use as the raw materials for the manufacture of food (pages 120 ff.). Meantime the various materials included in the above series of reactions may permeate wood or masonry or may accumulate in drinking or other water, changing the color, firmness, strength, taste, or other property.[53]

Oxidation of Iron

The classical researches of Winogradsky,[54] followed by the later and somewhat more extensive, if less inspired investigations of Molisch, have shown that iron may also undergo oxidation in the metabolism of bacteria. Thus soluble compounds of iron in water supplies and water pipes may furnish fuel for iron bacteria in the walls of whose cells ferric oxide and hydroxide become precipitated. The color and flavor of the water may thus be adversely affected, plumbing, masonry, etc., exposed to the water may become stained, and even the diameter of the pipes decreased. Great accumulations of iron in nature may also be the result of the oxidation of iron by the so-called iron bacteria.

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[53] See Ward, H. B., and Whipple, G. C., *Fresh-water Biology*. New York, 1918.

[54] Winogradsky, S., Ueber Eisenbakterien. *Bot. Zeitung*, 1888. Molisch, H., *Die Eisenbakterien*. Jena, 1910.

The rusting of iron to ferric hydroxide, which occurs almost universally at ordinary temperatures in ordinarily moist air, releases 95.5 calories per gram-molecule. This same amount of energy with the evolution of light as well as heat, is liberated with great rapidity at the high temperature of the blast furnace and in an atmosphere of oxygen in the lecture experiment of the burning watch-spring. At the temperature of living bodies, however, the oxidation of iron and the release of energy would be too slow to meet the needs of the organisms were the chemical action not accelerated by a catalyzer. What the catalytic agents are in the case of the iron bacteria is not yet determined; nor are we justified in assuming the total yield of energy above suggested because undoubtedly partly oxidized compounds and not metallic iron are the materials of metabolism.

While the iron bacteria are few in number of species, and in fact form only a small fraction of the total of living things, their relation to the metallic element entering at the present time most intimately and completely into human life in all its activities, physiologic, sociologic, economic and competitive, make it imperative that they be reinvestigated, with imagination as well as skill.

It is known (see pages 121, 68–79) that iron is indispensable in the nutrition of green plants as well as of animals. While the iron is absorbed in the form of simple salts, it undoubtedly undergoes change in the living cell, perhaps forming colloidal organic compounds, insoluble and therefore immovable and not further usable when the organisms containing them die. The restoration of iron, therefore, to the soil in forms suitable for absorption and use as food materials is as necessary as the corresponding parts of the other "cycles" of the constituent elements of food. The restoration of iron is accomplished apparently by the various iron bacteria, the nutrition and oxidative metabolism of the successive series of which, in the soil and in water, result in breaking down the complex, perhaps colloidal, carbon compounds, to inorganic ferrous compounds and the oxidation of these to ferric, in the final forms of sulphate, chloride and nitrate. Ferric carbonate (bog iron ore) is more or less completely removed, at least for long times, from further part in metabolism.

Oxidation of Nitrogen

While the restoration of carbon, hydrogen, sulphur and iron to the soils and the waters of the earth in forms usable as raw materials for the manufacture of food by plants, is of the utmost importance both theoretically and practically to man both as living organism and as agriculturist, he ordinarily considers the completion of the nitrogen cycle as second in importance only to the completion of the carbon cycle. They are both accomplished by the destructive, mainly oxidative, metabolism of bacteria of certain well defined species, using as their fuel and food the products of many bacteria of decay. Whereas the nitrogen of the soluble soil nitrate is made a part of a protein molecule apparently by the constructive metabolism of a single organism, perhaps of a single cell, through the changes previously suggested (pages 96–

97), the re-formation of nitrates in the soil and in water involves the destructive metabolism of a whole series of organisms, the one being dependent upon and using the products of another. This succession may best be visualized if it is briefly sketched.

The organism which dies, whether plant or animal, consists of insoluble proteins as well as of soluble nitrogenous compounds of carbon. While the soluble ones are immediately available as food for one or another organism, the proteins must be digested (see pages 206 ff.). If digestion be followed or accompanied by more or less complete oxidation there will be liberated a corresponding amount of energy and simpler and simpler compounds will be formed. Some of these partly oxidized compounds give the offensive odors of putrefaction, some may be otherwise offensive, in consistency for example or as poisons, and each is the product of bacterial or fungous or other destructive action on material at one time a part of a living organism. The final result of the destructive metabolism of the organisms of decay is the liberation of ammonia (NH_3) or the formation of ammonia compounds (*e.g.*, carbonate, sulphate, nitrate, phosphate and chloride). While these can be used to some extent as raw material for the manufacture of proteins, the nitrates are much more valuable than ammonium salts as sources of nitrogen (page 89). The production of nitrates from ammonia salts is accomplished in the soil[55] and in the sea[56] by bacteria, the essential characteristics of which were first described by Winogradsky, who overcame the obstacles to pure experimental culture of these peculiar organisms. He determined that the process is carried on in two stages, consisting in the oxidation of the ammonia liberated in the decay of organic nitrogen compounds, to nitrite, and the further oxidation of the nitrite formed from the ammonia. Two new genera of motile soil bacteria, described and named by Winogradsky as *Nitroscococcus* and *Nitrosomonas,* occurring in all natural soils, oxidize the ammonia to nitrous acid. This is acted upon by *Nitrobacter,* which oxidizes nitrous to nitric acid. The nitric acid is neutralized by the carbonates of the soil. The reaction, taking place in these two stages, is as follows, using ammonium sulphate as the source of ammonia in the soil, as it was in Winogradsky's experimental cultures:

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[55] Winogradski, S., Recherches sur les organisms de la nitrification. *Ann. de l'Inst. Pasteur*, 4, 5, 1889–91. Zur Mikrobiologie des Nitrificationsprozesses. *Centralbl. f. Bakteriologie*, 2te Abth, II. 1897.

[56] Reinke, J., Die zur Ernährung der Meeresorganismen disponiblen Quellen an Stickstoff. *Ber. d. d. bot. Geselschaft*, 21, 1903.

$$(NH_4)_2\ SO_4 + 3O_2 = 2HNO_2 + H_2SO_4 + 2H_2O$$

$$2HNO_2 + O_2 = 2HNO_3$$

$$(2HNO_3 + \text{any carbonate} = \text{a nitrate} + CO_2 + H_2O$$

The release of energy in these processes has not been measured but it is theoretically as follows:

NH_3 to N and H_2O	90.6 Calories per gram molecule
Ammonium nitrite to H and H_2O	71.8 Calories per gram molecule
Therefore, NH_3 to nitrite	18.8 Calories per gram molecule
Nitrite to nitrate	37.2 Calories per gram molecule

As has been previously pointed out (page 93) these organisms are able to fix CO_2 in darkness as well as in daylight. The direct source of needed energy is thus shown to be the oxidation of ammonia compounds and derivatives. While the nitrate bacteria are said to be autotrophic, it is evident from the foregoing description that they are so only in respect to carbon, and that they are not so in respect to nitrogen. The only completely autotrophic organisms are green plants, which manufacture their own food and fuel at the expense of external solar energy. The nitrate bacteria manufacture their food at the expense of fuel which they must obtain ready made. In this respect they are, as we have seen, like the various iron, sulphur and hydrogen bacteria, and all the dependent organisms — saprophytes, parasites, and animals — which use unsaturated carbon compounds as sources of energy.

The metabolism of all living organisms which releases energy for their use does so by oxidizing unsaturated or oxidizable compounds or ions of carbon, hydrogen, sulphur, iron and nitrogen. In certain instances the oxidizable substance is so simple that there can be no question as to where the new oxygen is attached, *e.g.* in the oxidation of carbon monoxide to dioxide.[57] There are bacteria said to oxidize marsh gas, methane, CH_4.[58] This inflammable gas is a product, along with CO_2, CO, NH_3, etc., of bacterial decomposition of plant and animal remains in the mud of small ponds and stagnant pools. Both the H and the C must take up O if the gas is to burn completely, and the yield of energy will be correspondingly large. In the other substances oxidized in plant cells, oxygen may unite with one or another radicle, unite with the H, C, S, Fe, or NH_3 ions, in each instance liberating energy to be used by the living cells, whether in operating or maintaining or enlarging the living machine. The rate of oxidation in any organism will depend upon external and internal factors such as temperature, the proportions of oxygen in air and water, especially of the water within the cell, the nature of the oxidizable material, and the presence of suitable catalysts in due amounts. The phenomenon of metabolism for energy release, therefore, is made up of many variables, with only the one common feature implied by its name, the release of energy.

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[57] Kaserer, H., Die Oxydation des Wasserstoffs durch Mikroorganismen. *Centralblatt f. Bakteriologie,* Abth. 2, 16, 1906.

[58] Söhngen, N. L., Ueber Bakterien welche Methan als Kohlenstoffnahrung und Energiequelle gebrauchen. *Centralblatt f. Bakteriologie,* II, 15, 1906.

This product in certain instances seems so excessive that one is forced to wonder whether the release of energy, beyond a certain point at least, is not merely incidental to the removal, by oxidation, of substances which would become injurious if not removed, the excess of energy being readily removed by radiation, exhalation, and water conduction, according to the nature and habitat of the organism. Thermogenic bacteria and moulds [59] carry the liberation of heat to the most striking degree, with no evident advantage to themselves, though man may make use of this phenomenon for warming outhouses, cold-frames, etc.

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[59] Boekhout and De Vries, O., *Centralblatt f. Bakteriologie,* II, 23, 106 +. Miehe, H., *Selbsterhitzung des Heues,* Jena, 1907.

VIII

IRRITABILITY

The Mechanical Influences

We have been concerned in the preceding chapters with the phenomena which provide the living plant with matter and with energy, with the material for the construction and maintenance of its body, and with the energy requisite for its operation. We have devoted little attention to the circumstances in which the plant builds and maintains itself, and lives as a self-operating mechanism. It is obvious, however, that no real understanding of living organisms, nor of the chemical and physical changes and conditions within them or produced by them, can be attained without some comprehension of the world in which we live. Furthermore certain of the so-called "vital phenomena" are so evidently affected by minor changes in their surroundings that an analysis of the environment is plainly called for.

The environment of all things on this earth is composed of living as well as of lifeless things. The living factors of any environment, the individual plants and animals, are not only working with the matter and energy of their surroundings but are competing with each other according to the degree to which they are crowded together in any given area. They are correspondingly struggling for existence. They are competing for a "place in the sun" or for other positions, not only of advantage but also of possibility. In the comparative comfort in which many persons live the phrase "struggle for existence" is as meaningless as it once was hackneyed. In a new country the scantiness of population, so far as a single species is concerned, may reduce the competition to such a degree as regards certain of the necessities of existence, that the reality of the struggle is not evident. We are inclined to think that, while human life may be more laborious in the country, it is less hazardous, the struggle for existence is less keen, than in the city. While the farmer's competition with his own kind may be less sharp, his competition with the enemies of his crops is far keener than the city man's struggle against parasitic plants or predatory animals of other kinds than his own.

Presumably then, there is such a system of checks and balances in the different parts of Nature that, where conditions have long continued unchanged, there is an established order, the parts of which are so adjusted to each other that their presence and their performance are, in a sense, automatic. When the violence of nature — flood, fire, tide, tornado, or pestilence — or the violence of man in his processes of agriculture, engineering, commerce, and war — changes the established balance, a readjustment of the components of the environmental complex necessarily takes place. Competition then becomes free, for a time at least.

Only less in degree, though similar in kind, is the effect of introducing a new component into a collection of already established species or individuals. When one makes a lawn, say of blue grass and white clover, on land up to that time uncultivated and supporting a mixed vegetation of herbaceous native plants, one attempts to displace all these "weeds" by the cultivated immigrants. Their struggle for existence succeeds if man is sufficiently assiduous in the weeding. If then into such an established lawn, one plant a small, slender, weak specimen of *Sequoia*, both *Sequoia* and lawn constituents find themselves for the first time in competition for water, light, raw materials, room. Such is the competition that one sees on the great scale in nature, at the edge of the forest, where forest and grassland meet, a competition altered for both contestants if a third party to the struggle come in. This is the case where a pioneer farmer plants a field with corn or other grain in his forest clearing; or, in the case of the lawn, when some other tree is later planted to share the materials and conditions of existence with the *Sequoia*, grass, and clover. The circumstances thus suggested are repeated in every family in which children are successively born, the conditions necessarily being different for the second and for each following child than they were for the first, the first and second together, etc. To these considerations as affecting all living organisms, we shall return for more detail later.

The word environment ordinarily suggests its lifeless components, the soil, the air, warmth, moisture, etc. These are, however, only a few of the unnumbered factors which compose the surroundings of all things, lifeless and living, thereby controlling their existence, and limiting their behavior. Analyses of the environment are few and imperfect,[1] for a complete catalogue of the universe is impossible and few have attempted to make even a partial list. If one essay a beginning, one sees that the environment is composed of factors mechanical, chemical, and radiant. In amplification of Henderson's conception of the environment — "the world of our senses is a world of matter and energy, space and time" — we may list some of these factors and then proceed to consider how plants grow and reproduce themselves under their influence.

The mechanical influences include winds, waves, water currents, gravity, contact, and injury. The chemical influences are exerted by water and by all the other constituents of the world which unite in any way with others. Water and many of these other substances may also exert purely mechanical influences, as the first rubric indicates. The radiant influences are those which we call heat, light, and electricity, the effects of which may show themselves as mechanical or as chemical, but which operate by means of their own energy of motion. In this category would come radium, radium emanation, and X-rays, the influence of which upon plants and plant processes is, as yet, by no means clear. Between the fatal effects which are produced by considerable exposures, and the possible influence of slighter exposures upon cell division, locomotion, and fertility, there may be all gradations.[2] Except as they have been studied as therapeutic agents in the treatment of diseases due to known or suspected infections (tumors, cancers, arthritic joints, etc.), they have been played with rather than subjected to serious and exhaustive study. The philosophical reason for this is not without interest and significance, namely that, as the practical value of such knowledge is not evident, research has waited on curiosity unstimulated by necessity, and no one so possessed has yet completed a thoroughly scientific study of the subject.

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[1] See Henderson, L. J., *Fitness of the Environment*. New York, 1913.

The operation of these factors is as diverse as the factors themselves. It may be constant, uniform, irreversible, inescapable; it may be periodic or occasional, varying in speed, intensity, direction; it may be entirely avoidable. Obviously, these characteristics of the different environmental factors bear not only upon the behavior of all living and lifeless things, but also upon our ideas regarding the character and behavior of living organisms as well as of lifeless things.[3] Gravity, water, air, the components and characteristics of which are constant, unchanging, and inescapable, constantly exert unchanging and inescapable influences upon everything; whereas light, heat, and electricity, and the chemical compounds in the world about us, act periodically, occasionally, or not at all, according to exposure to them. Their control over state and action corresponds precisely with these characteristics.

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[2] Zwaardemaker, H., On Physiological Radio-activity. *Journ. Physiology,* 53, 1919. Blackman, V. H., Radio-activity and Normal Physiological Function. *Annals of Botany,* 34, 1920. Hamberger, J. J., Die Zwaardemakersche biologische Radioaktivität. *Biochemische Zeitschrift,* 108, 1920. Stoklassa, J., Ueber die Radioaktivität des Kaliums. Three papers in *Biochemische Zeitschrift,* 108, 1920. Molisch, H., Ueber das Treiben von Pflanzen mittels Radium. *Sitzb d. Kaiserl. Akad. d. Wiss. in Wien,* 121, 1912. Williams, Maud, Observations on the Action of X-rays on Plant Cells. *Annals of Botany,* 37, 1923.

In the conception of living protoplasm and living organisms as systems consisting of colloids, fats, electrolytes, and water we have a partial basis for understanding the sensitiveness or irritability of living organisms; but until knowledge is complete enough to enable one really to understand the behavior and the characteristics of such common and simple things as table salt (NaCl) no one need delude himself into thinking that he knows why living organisms do as they do. By this is not implied any philosophical, still less scientific, need of the ideas of vitalism,[4] but merely the fact that knowledge of the physics and chemistry, and hence of the physiology, of living beings is still so far from complete that the quest for more knowledge must be full of surprises and rewards. We may, however, form a dim notion of the basis of irritability. Thus we know: (a) the instability, mechanical and other, of protoplasm or of any other system of water, colloids, electrolytes, and fats: (b) we know something of the kinetic energies and the electrical charges of the molecules, atoms, and ions of the components of this colloidal system: (c) something of the number, variety, and speed of the chemical changes taking place among the components of this colloidal system: (d) and something of the number, variety and speed of the chemical changes taking place between the components of this colloidal system and the substances within it. The processes comprising (c) constitute the so-called *basal* metabolism while those comprising (d) constitute the *functional* metabolism of living organisms. In (a) and (b) it is implied that irritability is a function not of living only or of protoplasm only but that, according to the terms of expression, it is a function or property of matter. When we attempt to conceive the behavior of living masses of matter in the same spirit in which we conceive and express the behavior of lifeless masses of matter, we realize that behavior is a consequence of composition and structure, and that its cause and consequences are presumably the same in all instances in which substance and circumstance are the same, that in very many instances variation, heredity, and the survival of the fittest are not any more real in the case of plants or animals, than in common salt. The reason for these assertions will become clearer as we consider various factors of the environment and the behavior of living organisms in relation to them.

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[3] Peirce, G. J., Certain Undetermined Factors in Heredity and Environment. *Amer. Naturalist*, 38, 1904.

[4] Driesch, H., The Science and Philosophy of the Organism. London, 1908.

I

Winds, Waves and Water Currents

In the descriptions of the ecologists[5] one will find information in regard to the molding of trees exposed to prevailing winds. Mountain passes, narrow valleys ("draws"), the tops of tree-clad dunes, and similar places, show trees which are strikingly one-sided although the trunk may be quite normally erect. The branches grow in length much less on the side toward the prevailing wind than on the side away from it. Examination of the trunks of such trees discloses, in certain instances, that the bark is smooth and thin on the side toward the prevailing wind while it may be thick and rugged on the leeward side. On a Sierra pass which I know, the reason for the smoothness and thinness of the bark on the windward side of the trunk of the pines is the purely mechanical one of abrasion, the wind, armed with snow, sleet, and rain drops, cuts and rubs off the dead friable outer bark. If there is any stimulus in this case, the reaction consists merely in production of bark fast enough to prevent injurious abrasion. When such trees are felled their growth in thickness is found to be excentric, corresponding with the dimensions of the dome of foliage. This one might expect; but the root system, quite sheltered below ground from direct action of the wind, shows equal excentricity. The major growth of the roots is on the side opposite to that of the branches of the stem above ground. Thus, on a dune on the California seacoast, one finds the branches, say of Monterey pine, growing more on the landward side of the tree trunk, but the roots growing more on the seaward side. Analysis of the particular factors involved in such a situation shows that the wind *pushes* against the seaward growing branches of the stem or trunk while it *pulls* the landward branches inland. Depending upon the temperature and humidity of the air and its rate of movement, the wind will take larger or smaller quantities of water by "transpiration" (see page 146) from the leaves and branches of both the seaward and the landward sides. It is hard to conceive that there will be any considerable difference in this respect between the two sides. A difference has, however, been alleged as the cause of the asymmetry so characteristic of trees deformed by strong sea winds. There is the obvious possibility of salt being deposited as spray on the branches and foliage, naturally more on the seaward than on the landward side; but as the deformity under prevailing wind is not confined to the borders of bodies of water of any sort, salt or fresh, some other influence must be involved.

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[5] Coulter, Barnes, Cowles, *Text Book of Botany*, Vol. 2, p. 734, 1911. Bernbeck, O., Der Wind als pflanzenpathologische Faktor. *Bot. Jahrb.* 45, 1911.

Mechanical pressure, and traction, on the windward and leeward sides respectively, are exerted by the wind. To this pressure and pull the growing branches must respond. Experiment showed, long ago, that pressure[6] and pull[7] both check growth. Continuous or repeated pressure may result in a permanent condition of smallness. This is perfectly familiar in the Chinese woman's foot, the prostrate dwarf forests at mountain heights close to timber line, and in plants growing in crevices in rock. On the other hand, while the first reaction to traction is a checking of growth, growth is increased both in length and thickness by continued and increasing tension, as is shown by the stalks of growing and pendent fruits.[8] There has been singular confusion in the treatment of the subject by successive authors, although experience proves that extension follows tension.

Applying these considerations to the behavior of the limbs of trees exposed to prevailing wind, we may conceive of their inequalities as being due to the pressure and the pull applied by the wind. This conception is strengthened by consideration of the behavior of the roots. Deferring till the section on the influence of Gravity (pages 235–261) a consideration of the general condition of the root, we can readily see that wind blowing upon the parts above ground may rock the parts below or may exert a prolonged if not constant pull upon one or another part of the root system. The pressure and pull of the wind upon limbs and trunk will inevitably be communicated to the roots below. This may constitute merely the occasional stimulus which we may call exercise, and to which the plant responds by developing greater strength, or it may constitute a condition (tension) which the root meets by corresponding growth, the corresponding growth being in the direction against the wind.

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[6] Newcombe, F. C., The Influence of Mechanical Resistance on the Development and Life Period of Cells. *Botanical Gazette*, 19, 1894.

[7] Hegler, R., Ueber den Einfluss des mechanischen Zuges auf das Wachsthum der Pflanze. *Beiträge zur Biologie der Pflanzen*, 6, 1893.

[8] Pieters, A. J., Influence of Fruit Bearing on the Development of Mechanical Tissue in some Fruit Trees. *Annals of Botany*, 10, 1896.

One should distinguish carefully between a purely mechanical result of wind action and the irritable reaction to prevailing wind above referred to. The former is often seen, particularly perhaps in parts of California where, when the ground is softened by heavy rain, the whole platform of roots on which a tree stands may be tipped by the action of heavy wind upon the trunk and branches, the stem becoming oblique and the branches of one side, now become the upper side, growing upwards. This is strikingly true of the live oaks (*Quercus agrifolia*) the shallow roots of which form a wide platform close below the surface of the soil. As these conditions of wet soil and high wind generally coincide in this region, during the storms of the rainy season (winter), one commonly sees these trees, evergreen and therefore exposing the maximum sail to the south wind, leaning northward with a uniformity which suggests their being on the march to San Francisco.[9] This purely mechanical tipping results in such changes in the relations of the parts to gravity (see pages 252–253) that changes in form ensue as a result of the stimulus of gravity, not of wind.

Waves and tides have not been studied experimentally in their mechanical relations to plants. It may be inferred that they produce movements which stimulate the plants exposed to them. The plants, and the animals, living attached to rocks, cliffs, piles, etc., exposed to surf and swiftly running tide must attach themselves very rapidly to the surface on which they grow. This attachment is probably the reaction of the spore or fertilized egg to the stimulus of contact with the rough object (see pages 261 ff.); but the subsequent development of such a plant as *Postelsia,* the Sea Palm, for example, is greatly influenced by the pounding, pushing, and pulling of the waves and currents. The most vigorous Sea Palms are those living in the most exposed positions. While it is true that the number of possible competitors is less in such situations than in that most densely populated part of the earth's surface, between the tidemarks in more sheltered places, it is also true that the *Postelsia* plants living in the less exposed rocky surfaces are also less strong, less large, less vigorous. Anatomical study of plants of the same age in different situations confirms this general conclusion.

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[9] Cannon, W. A., Tree Distribution in Central California (illustrated), *Pop. Sci. Monthly*, 1914. Jepson, W. L., *The Silva of California*. University of California Press, 1910.

In the plants living submersed in streams or tidal runs we have interesting examples of irritable response to water currents. It is obvious that the leaves and stems of eel-grass, *Potamogeton,* and similar flowering plants, as well as the filaments and fronds of *Cladophora, Fucus, Nereocystis,* and the other attached algæ, will be subjected to pull and will be mechanically carried by the current; but to holdfasts and root systems the filaments, fronds, and stalks will transfer the pull according to its intensity. Thus holdfasts may be conceived to develop in consequence of the stimulus of mechanical strain and in proportion to it, and the root systems grow upstream in the mud of the river bottom. These roots are responding to the same mechanical force — pull or traction — as the roots of wind-blown trees, and their reaction is similar. The active force applies a strain to the leaves, branches, stems, and stalks;

this is transmitted to holdfast and root system; both of these respond to the pull, tug, drag or traction. The growing tip of each root or rootlet and of each branch of the holdfast, receiving this pull, reacts by growing in the opposite direction. In conformity to the general botanical vocabulary this would be called a negative reaction. The stimulus, furthermore, applied generally and extensively along the whole organ, is generally perceived instead of being perceived only by one especially sensitive part; but the response is confined to the growing region, the direction of response is determined by the direction of pull, and the extent of the response is proportional to the intensity and persistence of the stimulus.

The behavior of the roots which break through the bank into a stream also illustrates purely mechanical effects or reaction to mechanical stimulus. If immediately after breaking through the bank the few millimeters of root are in swiftly running water, the tips may turn and grow upstream. If, on the other hand, the roots grow to such length that they are swept downstream by the current, the result is purely mechanical; there is no physiological response. The former response is termed *rheotropism.* It appears that by no means all plants respond to water currents flowing against their roots in experimental cultures,[10] and the inference has been drawn that it is a phenomenon of no general significance in nature. Recent experiments have tended, if anything, to confuse the issue still further.[11] Newcombe's carefully conducted experiments demonstrated the reaction of the roots of several species of common herbaceous plants to water currents of sufficient speed. Stark showed that among those plants were some known to be sensitive to contact. Hryniewiecki apparently found that the composition of the aqueous solution bathing the roots, or, in more modern terms, its hydrogen-ion concentration, determines whether the roots will react or not. The last named investigations throw a new light on the problem, placing it merely with other reactions known to be dependent upon the health of the cells and tissues, a state of health which is now known to be very dependent upon the delicate balance of acids and bases in the environment and in the cells themselves (see pages 339–340). Stark's work may be misleading, for, as Newcombe says, although there is pressure against the roots by the stream of water, thigmotropism (sensitiveness and reaction to contact or pressure) has not been demonstrated in roots.

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[10] Newcombe, F. C., The Rheotropism of Roots. *Botanical Gazette,* 33, 1902. The Sensory Zone of Roots. *Annals of Botany,* 16, 1902. Stark, P., Studien über traumatotrope und haptotrope Reitzleitungsvorgänge. *Jahrb. f. w. Botanik,* 60, 1921.

[11] Hryniewiecki, B., Untersuchungen über den Rheotropismus der Wurzeln. German abstract of the Russian paper in *Zeitschr. f. Botanik,* 1, 1909.

Let us, then, ourselves attempt an analysis of the phenomenon. Let us imagine a root growing in damp air vertically downward into a suitable aqueous solution which is in motion. The downward growth of the root is in response to gravity, the movement of the water current at right angles to this, namely horizontal. The course which the root will take will be a resultant of these two mechanical forces. If the root were lifeless, merely falling downward through the water, the resultant of the action of gravity and of the stream would be a course both down stream and toward the bottom. But the root is alive, reacting to gravity and to pressures and pulls. The resultant is then a course upstream and toward the bottom. As soon as the turn from the vertical is made the pressure of the current upon the root ceases to be as one-sided as possible and becomes more and more a pull along the whole surface and mass of the root. This makes the action of the water current upon the root more and more like the action of the wind current previously described, a pull to which the root responds in the opposite way as the stem. Rheotropism, therefore, and the response of roots to wind blowing upon stems and branches above ground, may be regarded as the same phenomenon, a response in both cases to traction.

Perhaps a few words may be said about the phenomenon named *rheotaxis,* much more evident in animals than in plants, if indeed it is to be found among plants at all. The term is applied to aquatic organisms which keep their heads upstream and tend to move upstream. Trout, salmon, etc., are said to furnish examples of the phenomenon, though one may ask the zoölogist whether the relation to oxygen and to other useful materials in solution in the water, and the structure of the gill system may not partly also determine the position of fish. The direction and velocity of the wind will also determine, mechanically and otherwise, the position and direction of flight of birds, butterflies, etc. Among plants, however, the small size of the motile ones makes the phenomenon far from striking and far from significant, if it exist at all. Experiment may well be made, however, by the curious upon diatoms and *Oscillatoria* as well as upon other motile algæ.[12]

The Influence of Gravity

Whatever may be one's mathematical or philosophical conception of gravity, we may define it for the purposes of this discussion as "the attraction of masses upon each other." This attraction is proportional to the masses and inversely proportional to the square of the distance between them. The earth being the largest of the masses with which we have ordinarily to deal, gravity is often spoken of as "the pull of the earth," and it is to the earth that we see bodies fall. It

[12] Gerhardt, Karl, Beitrag zur Physiologie von Closterium. *Inaug. Diss.,* Jena, 1913.

should be pointed out at once, however, that according to our definition, all masses attract each other, and all the components of any system, as well as the system as a whole, attract each other. In a system the components of which have different specific gravities, the masses correspondingly attract each other and correspondingly act upon other systems. Then the drops of oil, grains of starch, vacuoles of cell sap, the nucleus, the cytoplasm, and chromatophores, and the other components of living cells, are individually attracted by each other and by the earth, the attraction of which, correspondingly, is the sum of the separate attractions of its components.

Furthermore, if masses and distances continue unchanged, the action of gravity is necessarily constant, uniform, inescapable, and irreversible, although it may be resisted. These axiomatic assertions are as important as they are ordinarily ignored; for if our definition of gravity be correct, it goes without saying that gravity is one of the factors of the environment the importance and the import of which it would be almost impossible to exaggerate. Every component particle of a living cell and living organism, plant or animal, is pulling upon every other component particle and upon the components of the world outside itself, and is pulled upon by the parts of that world. Thus, sperm and unfertilized egg, the cells which gave rise to them and the cells and organisms which they presently form, have been acted upon continuously from the beginning by gravity with the same force, in the same direction, always.

This force is sometimes expressed in mechanical terms as being equal to an acceleration in a vacuum of 32.2 feet per second squared. The value of this is demonstrated both as to actuating force, and also as to reliability and uniformity, in the various uses made of weights in the driving and regulating (pendulum) of clocks and clockwork of various sorts.[13] Its importance is proved by the injuries resulting from falls. The felling of trees in lumbering must be done with skill if the logs are to be unimpaired in value by their impact with the soil after beginning their descent with no motion from the position in which they are stayed by the mechanical system of the tree.

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[13] Peirce, G. J., Ein multipler Klinostat. Jahrb. f. wiss. Bot., 56, 1915.

Granting the magnitude, constancy, and uniformity of the force of gravity, it is obvious that it can be opposed and is opposed in a great variety of ways which, however, for convenience of discussion, may be reduced to a single general principle, namely the resistance afforded by the intervening medium. It goes without saying that, in a cell, the solid particles of greater specific gravity than the cytoplasm — such as the nucleus, starch grains, and crystals — would all fall to the bottom of the cell, and all the lighter components — such as drops of fat or oil — would fly to the top, were it not for the opposing intervening cytoplasm. The cytoplasm is therefore pressed upon, downward and upward, at all times, by the respective components and contents of the cell. The drag on an organism as a whole is similar to the drag upon its parts: it is continuous, penetrating, universal, but opposed.

What is true of the cytoplasm, is true also of the cell wall and of cell aggregates, but we may more clearly understand this if we first consider other opponents of gravity, namely, the air, water and soil.

According to the principle of Archimedes a body in a fluid is buoyed up with a force equal to the weight of the fluid it displaces. The buoyant power of air is slight, that of water 700–800 times as great. The supporting power of the soil, while varying with the nature of the soil, or rock, is many times that of water. Examination of land plants discloses differences in structure according to differences in habit and habitat. Prostrate forms, supported directly and at frequent intervals, are structurally weak. The parts above ground of erect plants are only indirectly supported by the soil, are buoyed up only slightly, and are mechanically strong, their crushing strength, however, being proportionally greater than their tensile strength. The tensile strength of their roots, on the other hand, is proportionally greater than that of the stems. At the crown of the root and the base of the stem, in the region of maximum mechanical strain, one finds the maximum of mechanical strength.

A tall symmetrical tree, in a situation sheltered from wind, rests upon a platform of roots, either extending horizontally and close under the surface of the soil, or forming a system of tap-root and laterals.[14] In either case the total weight of trunk, branches and foliage is carried by the roots. Generally the roots are supported by the soil, but that this is not necessary is occasionally shown when the root system continues to carry a tree although the soil may have been washed out from between the parts. At all times the crown of the root is subjected to pressure, a pressure which grows with the plant and may be greatly and even suddenly increased by wind, snow, sleet, or even rain. This pressure is distributed from the crown of the root to its branches, but the major part of it is necessarily borne by the butt of the tree and the crown of the root. It may amount to a great weight, tons in fact, concentrated on a relatively small mass of tissue.

Study of the anatomy of erect plants discloses differences in structure coinciding with the differences in stresses. Thus, as the lumber dealer knows, there are pronounced differences in structure, strength, and weight between the upper parts of the trunk and of the butt in the black walnut. These differences cause the differences in value and price, black walnut butts being especially prized for gunstocks and being correspondingly costly. Similarly the butts of redwood trees, or the crowns of their roots, are extensively used for ornamental woodwork, small trays, bowls, etc., for which the rest of the trunk is quite unsuited. The greater hardness, bearing power, and other qualities are due to the thicker walls of the cells forming the butt or the crown, their smaller size, their more thorough lignification, their extensive attachment to each other, the crookedness of the grain, and perhaps to other qualities.

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[14] Cannon, W. A., Vegetation and Environment in California. *Plant World*, 17, 1914.

The position, direction, size and length of branches in a tree are determined by many influences in addition to those included under the term heredity. By this last is meant, or at least suggested, that a character so important to the taxonomist as the excurrent or deliquescent stem of a tree is fixed by heredity, that it is inherent in the tree itself. On the other hand, the position and other features of the branches on the stem are profoundly influenced and in part determined by external influences, of which wind, light, and gravity are the most obvious. We have discussed the influence of prevailing wind (pages 230–231). We shall presently discuss the effects of light, and we are so familiar with the symmetry of plants growing where neither prevailing winds nor unequal illumination can affect them, that we are accustomed to pass over this phenomenon without reflection.

The branches of erect and inclined stems spring in positions of maximum mechanical disadvantage from the parts which bear them. They grow out to exercise the maximum leverage against their supports. They carry their growing loads of foliage and fruit so that the maximum strain develops upon all the parts involved. Increase in strength requires increase in weight as well, and hence increase in strain. So far as an individual limb is concerned the only ways of meeting this condition are: (1) by perfect continuity of adequate mechanical tissues in stem and branch; (2) by the growth of a bracket on the underside of the limb, particularly at its base, and (3) by the growth of a stay on the upper side of the limb, also at its base.

The first of these methods is the least conspicuous and the most common, a method, the value and effectiveness of which is obvious, but the details of which become evident only when the methods of anatomy and microchemistry are applied to a study of the tissues involved. These will reveal the comparative length of cells and their direction, the thickness and hardness of their walls, and the number of mechanical elements at the base of a branch as compared with the parts farther along. The hardness, compactness and other characteristics of "knots" in wood demonstrate the difference between wood growing under great strain and what is known as "clear" lumber.

The third method is the less conspicuous and the more common of the other two. It is found wherever the outline of the stem merges in a curve into the upper line of the branch. Microscopic study shows that the mechanical tissues in this case also are better developed both as to the number and the character of the cells than nearer the tip of the branch. Differences in the age of the different parts do not alone account for these differences. They must be regarded as the responses of living cells to the stimulus of gravity.

The second method attains conspicuous development in certain well-known instances, confined, so far as my observation shows, mainly to trees of ancient origins. In the trees of tropical jungles one should be able to recognize this phenomenon on the great scale, but in the redwoods and cypresses of California, the Eucalyptus of Australia, one sees the extraordinary development of bracketing under branches horizontally extended.

On mature Monterey cypresses (*Cupressus macrocarpa*) for example one may see a thin plate of woody tissue, perhaps three or four feet in width and only seven or eight inches in thickness, extending from the under side of a horizontal limb to the side of the trunk below. Similarly the horizontal limbs of redwood (*Sequoia sempervirens*) are supported by thin brackets. A conspicuous example of this phenomenon is on the historic old redwood which is represented on the official seal of Stanford University. This tree, situated close to the railway on the bank of a creek, is the most conspicuous object for many miles from the ranch and the town to which it gave its name of Palo Alto. The lowest limb on one side of the tree is horizontal. It carries three erect branches at different distances from the trunk, and it is bracketed by a striking thin wide plate of wood.

The phenomenon which is called symmetry, as it reveals itself to the eye, consists, in fact, in a balance of weights or of strain, in different parts and on the different sides of plants. This is exhibited more conspicuously by trees but is no less real in small herbaceous plants. Furthermore, the balance of weights on the trunk lessens the mechanical strains on the root system; but any lack of balance in the parts above ground inevitably applies corresponding strain upon the parts underground. These strains correspond exactly with those strains resulting from wind action as discussed previously (pages 230–231); they consist in pulls, pushes, pressures; they originate in the action of gravity; and to them the living organism reacts. The reaction consists in the distribution of material in such ways as to balance weights and strains.

The evidence that gravity is the stimulus to which plants react in the ways above described is furnished by plants in which the load is carried mainly by such supports as trellises, walls, and frames, and by parts bearing rapidly developing loads.

In horticultural practice plants may be carried by walls or other supports for a variety of reasons. In England grapes, peaches, etc., are grown on south-facing brick house-walls for the sake of warmth. In France, Belgium, Holland, fruit trees are cultivated on fences (espaliers) to economize space. In this country we may grow tomatoes on frames in order to keep the fruit from harm. In any case part of the weight of the plant is carried by the support, the mechanical strain is reduced, the action of gravity is offset by other means than those which the plant would otherwise be forced to provide, or to fail. Examination of cross sections of branches so supported, especially of the butts of the branches where ordinarily maximum strain and maximum reaction occur as cause and effect, will disclose that the plant, while developing the usual amount of conducting tissue, has developed only the requisite amount of mechanical tissue, namely less than usual. The wood of such trained trees is weaker than of ordinary trees of the same species.

The development of mechanical tissues under increasing loads is a phenomenon of annual occurrence. We see this in the stalks of flowers and fruits,[15] and we see it again in the formation of wood in so-called "annual rings." As to the first, experiments may easily be conducted which will demonstrate the part played by gravity, *i.e.* the weight or strain to be borne, in determining, within the limits fixed by heredity, the development of flower and fruit stalks. Relieving the stalk of the larger common *Erodium*, for example, of the weight of the cluster of flowers and fruits by suitable tying to a small stake, is followed by the usual development of conducting tissues but by less than the normal development of mechanical tissue (hard bast fibers). What occurs quickly in this short-lived annual necessarily occurs in perennials as well, and in them the development of the mechanical tissues is not confined to the stalks of flowers and fruits, but may be traced through the twigs and branches back to the main trunk of trees or shrubs. The breaking of highly cultivated fruit trees, both citrus and deciduous, under the increasing load of developing fruit, offers a familiar example of the failure of the plant to meet the annual strain. This failure may be due, in the first place, to such a method of shaping the tree as may exaggerate the mechanical weaknesses above indicated (see page 239 as to manner of branching), and it may be due in the second place to pruning for production without due attention to strength.[16] Ordinarily in nature, and in the best conducted orchards, the mechanical strength of the growing trees equals the annually increasing loads of fruit. Obviously this condition can be maintained only by such correlation of growth and need as can be accounted for only on the basis of stimulus and reaction, the stimulus of gravity reacted to by the living organism.

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[15] Pieters, A. J., Influence of Fruit Bearing on the Development of Mechanical Tissue in some Fruit Trees. *Annals of Botany*, 10, 1896.

A still more general though less evident formative influence of gravity upon growing plants is found in the phenomenon of annual rings in the perennials of so-called temperate zones. As shown by the experiments of Jost and many others,[17] as well as by observation, there is intimate connection between the putting out of leaves, the extent of their development, and the formation of wood. It has long been known that two rings of wood will be formed if the spring leaves are destroyed by late frost or by caterpillars. If the development of the

[16] See Bailey, L. H., *The Pruning Manual.* New York, 1916.

[17] Jost, L., Beziehungen zwischen Blattentwickelung und Gefässbildung in der Pflanze. *Bot. Zeitung,* 1893. Peirce, G. J., Notes on the Monterey Pine. *Bot. Gazette,* 37, 1904. Küster, E., Ueber rythmisches Dickenwachsthum. *Flora,* 111, 1918. See also Gothan, W., Die Jahresringlosigkeit der paläozoischen Bäume und die Bedeutung der Erscheinung für die Beurtheilung des Klimas dieser Perioden. *Naturw. Wochenschrift.,* 28, 1911.

leaves is seriously checked, as by wholesale galling, by atmospheric pollution (SO_2 for example), and even by excessive dusting, there will be corresponding deficiency in wood formation. On the other hand, if agricultural or horticultural practice includes periodic irrigation so that there are two or three sets of leaves formed per annum, as in the orange and lemon growing regions of California, there are two or three rings of wood added each year.

When one examines the wood produced in a single year by the growth in thickness of a twig, branch, or stem, one finds, as is well known, that the wood first formed in the growing season is composed of cells (ducts or tracheids) of considerable diameter and with relatively thin walls. These constitute the so-called " spring wood," which forms while the leaves are coming out of the winter buds and growing in size and thickness, requiring the maximum volumes of water and dissolved substances, foods as well as food-materials. The " spring wood " is, then, primarily a vascular tissue, carrying to the young leaves the supplies needed. With the increasing load of foliage, however, and in trees blooming and fruiting, the character of the wood changes, the new cells are smaller and become thicker walled, the tissue formed is harder and stronger. This constitutes the so-called " autumn-wood " which, however, is invariably formed very soon after the " spring wood " and indeed is generally completed before midsummer. This then, is another example of the formative influence of gravity, the mechanically strengthening character of the wood later formed each year being proportioned to the strain to which it is subjected.

In unusual situations it may happen that, instead of forming one or more rings of wood each year, there may be an occasional year in which none is formed. On a bank in the high Sierra of California on which willows grow, I once saw the willows remain completely covered throughout the summer by a great bank of snow which persisted into the second summer. No growth took place, no leaves opened, under the snow; the willows remained cold and dormant throughout one summer; but in the second summer the snow completely disappeared, leaves came out and growth took place as usual. Presumably such observations have repeatedly been recorded in the writings of Arctic and Antarctic travelers.

The explanation of annual rings thus given, depending upon observation and experiment, is quite different from explanations put forward earlier. Of these perhaps the one generally considered most probable invoked a tightening of the bark upon the soft growing tissues within, which resulted in their component cells remaining smaller than they otherwise might. In this hypothesis there are two defects, namely that the bark does not tighten at the time of formation of "summer wood" if at all, and that, if it did, it would not induce the cells to form thicker walls. This latter matter, in its various bearings, was carefully and fully worked out by Newcombe,[18] for he found that enclosing young growing stems, etc., in Plaster of Paris was followed by the cells remaining small, for lack of room to grow, but also thin-walled, because they were so completely supported by the plaster bandages. Timely removal of the bandages was followed by the development of the necessary strength through the thickening and hardening of the walls of cells already formed or, if necessary, of new cells.

On the basis of experience thus described, the explanation of the absence of rings in palæozoic woods, and the occurrence of rings in the fossil woods of tertiary deposits, would be accounted for by a physiologist as due to climatic conditions. In earliest geologic time these conditions were presumably as uniform as those now prevailing in the humid tropics. In tertiary times there prevailed, at least over the regions of fossil accumulation, conditions similar in their periodic change to those prevailing today in temperate regions. Thus annual rings are interpreted, not as signs of higher development,[19] but rather as the record of the exposure of the individual to different conditions from those prevailing earlier. Perhaps these conditions prevailed at the same time, but in another region, conditions alternately favorable and unfavorable, in frequently recurring periods, like those of the seasons in present geologic time.

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[18] Newcombe, F. C., The Influence of Mechanical Resistance on the Development and Life-period of Cells. *Botanical Gazette,* 19, 1894.

It should be recognized also that the habits of plants may have very direct bearing upon their form and strength. The trees of a forest, the components of chapparal, the constituents of thickets, and the members of all other close stands, such as corn in rows, so shade and shelter each other from light, wind, and various other influences that they take on characteristic forms. Upon these plants gravity acts comparatively simply. Trees of the open — oaks, elms, madrones — and trees of the forest are not only very different in type but also in habit. That this difference in habit is not due entirely to differences in type but, on the contrary, to differences in relation to the formative factors of the environment, is indicated by the corn plants in the rows and those growing solitary from kernels accidentally dropped; the pines, firs, and *Eucalyptus* of close stands and those of the open. Bamboo and the other grasses, *Equisetum,* the cat-tails, rushes, etc., and the Calamites of times past, are examples of plants not only of gregarious habit, but of habit made necessary by structure and form in relation to gravity. The investigation so auspiciously begun by the German botanist Schwendener[20] in his study of the mechanics of structure in the monocotyledons, has not been extended, as would be desirable, by corresponding studies of other groups of plants. The structure which, while providing for continuous or periodic growth, according to climatic or other conditions acting as stimuli, also provides for branching in a medium of very slight buoyant power, namely the air, must necessarily be very sensitive and very able to react to the constant force which attracts any ponderable particle. In the plan and in the component structure of the Gymnosperms and of the perennial Dicotyledons, this condition is realized. Indeed, the sensitiveness to gravity as a formative influence which is revealed by the shape, size and structure, direction and balance, of the parts and of the whole of a tree, is quite as marked and quite as important as the reaction of roots and stems to gravity as a directive influence.

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[19] Jeffry, E. C., *The Anatomy of Woody Plants.* New York, 1917.

The familiar fact that, as a rule, roots grow downward into the soil, stems upward into the air, leaves and the branches of both stems and roots more or less horizontally, has been so extensively and intensively studied that a "literature" has accumulated entirely disproportioned in bulk and technicality to the literature of other subjects exceeding it in importance and even in significance. The reason for this is that roots are externally simple in form, tolerant of a considerable variety of conditions easily imposed, and their reactions to the stimuli deliberately and consciously applied are generally evident within the time limits set by the human eye and by human impatience. But while the phenomena of geotropism, in roots principally, have been described very fully and in an ingenious vocabulary, the actual mechanism of perception and of geotropic response is not determined, although hypotheses are not lacking.

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[20] Schwendener, S., Das mechanische Prinzip im anatomischen Bau der Monocotylen. Leipzig, 1874.

Locomotion is possible in animals and plants only when the action of gravity is sufficiently offset by the surrounding medium, air, water or soil. Locomotion through the soil is accomplished, as it is upon the soil, by taking advantage of the soil as a medium supporting the mass of the organism, but supplementing the buoyancy of the air by means of a skeleton. Locomotion in water does not require as a preliminary the substitution of any other medium. The zoöspores and gametes of aquatic plants swim in water, but the sperms of land plants must fall or be discharged into water before they can move by their own efforts. Plants have no means of so overcoming the influence of gravity that locomotion in air is possible. Their sperms, pollen spores, and seeds may be discharged into the air, but their fall can only be delayed; it cannot be prevented by any means which plants possess. Water is, then, the only medium the buoyancy and the resistance (viscosity?) of which are such as to make locomotion possible for plants and plant parts. Animals are otherwise adjusted to gravity and are able to move in air and in soil accordingly.

The directive influence of gravity, so far as plants are concerned, is then mainly upon growth. While its influence may be the same upon all parts of the body, the responses of the different parts may be directly opposite in plants as well as in animals. Thus while man habitually keeps his feet down and his head up, land plants do the same with their roots and stems respectively. Root and stem, like foot and head, are said to be differently *attuned* to the same force acting as a stimulus. While this is obviously true, the statement is not informing. In what does the stimulus consist, and how is a cell or an organ attuned to it? The history of plant physiology records different answers to both of these questions. As already indicated, the components of a living cell, have, among other properties, different specific gravities. The different contents as well as the different components are acted upon with different intensities by the same force. There are therefore necessarily different pressures, upward and downward, of the organic solids, volumes of solutions, drops of oil, mineral particles, etc. As every cell is formed by the division of its predecessor, these pressures are necessarily continuous throughout the generations of cells. In fertilization more substance is added to the egg by the entrance of the sperm, but the position is not necessarily changed. The fertilized egg divides, apparently in accordance with a polarity established by some external influence, of which light [21] and gravity [22] are the most common. In the fern, for example, four cells result from the first two divisions of the fertilized egg, the two lower of which form the foot (placenta) and the root, the upper two the stem and the leaf. There thus develop, in the embryo, a polarity which is continued throughout the life-time of the individual. Similar polarity is recognized in higher plants,[23] without, however, any more definite physical or morphological basis being known than in animals.

If it were true that all the lighter constituents of a cell are at the top, all the heavy ones at the bottom, and if the upper of the two daughter cells formed by horizontal division contained the lighter constituents while the heavy ones were in the lower, we could not fail to conceive how polarity arises: but so long as division provides an equal share of the contents of the mother cell to the two daughter cells, no simple conception is possible. This is equally true of cells, organs, organisms.

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[21] Kniep, H., Beiträge zur Keimungsphysiologie und Biologie von Fucus. *Jahrb. f. w. Botanik*, 44, 1907. Peirce, G. J., Studies of Irritability in Plants. *Annals of Botany*, 20, 1906.

[22] Campbell, D. H., *Mosses and Ferns*. New York, 1918.

[23] Vöckting, H., *Organbildung im Pflanzenreich*, 1878, 1884. Goebel, K., *Organographie der Pflanzen*, 2te Auflauge, 1913 plus. Haberlandt, G., *Zur Physiologie der Zelltheilung*. Sitzungsb. Berliner Akad., 1913–14.

Turning to the question of the stimulus itself, our definition of gravity indicates that the stimulus consists in the pressure or push of the parts, constituents, or contents of living cells upon each other. The classical experiments of Knight,[24] who sprouted seedlings on a horizontal revolving wheel and noted that the primary roots grew toward the circumference while the primary stems grew toward the center, are only too frequently cited as examples of the substitution of centrifugal force for the attraction of gravity. According to our definition of gravity, it is constant and inescapable. Centrifugal force may be deliberately employed in experiment to oppose gravity actively just as soil and other supports may be employed to oppose it passively. The positions of roots and stems are, therefore, the resultants of their reactions to both centrifugal force and gravity. This is perfectly clear when only moderate centrifugal force is employed in experiment, and is correspondingly obscured by the application of excessive centrifugal force.

Continued rotation of a plant upon a horizontal axis is followed by the root and stem occupying as nearly as possible the center of rotation but growing in opposite directions along the axis. Instruments designed for continued rotation of plant cultures for experimental purposes are called clinostats.[25] Many different forms have been devised, utilizing clock springs, weights, water and electric motors to actuate the mechanism. Several are obtainable from instrument manufacturers,[26] others must be built. All but one suffer from the radical defect that cultures can be experimented upon only in succession,[27] thus making differences in the conditions practically certain.

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[24] Knight, T. A., On the Direction of the Radical and Germen during the Vegetation of Seeds. *Phil. Trans. Roy. Soc.*, London, 1805–06.

[25] Van Harreveld, Ph., *Die Unzulänglichkeit der heutigen Klinostaten*

It has often been queried, but so far as I know never determined, whether a plant continuously rotated on a horizontal axis is not otherwise incapacitated from responding to the stimulus of gravity than merely because there is the fairly rapid succession of up and down and intermediate positions. Such change of position, occurring rapidly enough to accomplish the desired end of preventing root and stem from turning respectively down and up, may well be conceived to disturb conditions in a living cell to such a degree that, not only are the stimuli abnormally many and frequent, but the mechanism and the capacity of response (or reaction) are destroyed, not to be restored until after the clinostat has stopped. It may be argued that the experiments of Elfving,[28] F. Darwin,[29] and Fitting,[30] not to mention others, refute such a conception.

Elfving found by experiment that grass stalks which otherwise would not grow further in length, and would only turn

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für reizphysiologische Untersuchungen, Groningen, 1907. Went, F. A. F. C., *Over een nieuwen klinostaat volgens het stelsel de Bouter. Koninkl. Akad. v. Wetensch.,* Amsterdam, 1923.

[26] See Ganong's physiological apparatus, put out by the Bausch and Lomb Optical Co., Rochester, N. Y.

[27] Peirce, G. J., Ein multipler Klinostat. Pfeffer Festschrift, *Jahrb. f. w. Bot.,* 56, 1915.

[28] Elfving, F., Verhalten der Grassknoten am Klinostat. *Översigt af finska Vet. Soc. Förhandlinger. Bd.* 26, 1884.

[29] Darwin, F., On geotropism and the location of the sensitive region. *Annals of Botany,* 13, 1899.

[30] Fitting, H., Untersuchungen über d. geotropischen Reizvorgang. *Jahrb. f. w. Bot.,* 41, 1904.

up if laid horizontal, would continue to grow for some time if revolved on a horizontal axis on a clinostat; but these experiments do not throw any other light on this specific question than by showing that cells which would naturally be dormant are stimulated to quite abnormal activity. The result is a hyperplasia; and hyperplasia is frequently the result of mechanical irritation.[31] It is hardly necessary to cite examples here (see pages 261–295). But this experiment, with the constantly revolving motion of the plant, throws no light on the capacity of the plant to respond at once to gravity by upward growth of its stem.

In the experiments of F. Darwin the plumules of sorghum seedlings were inserted into horizontal glass caps which held the stem tips of the seedlings horizontal while permitting the roots to grow freely in the moist chamber. The result was spiral roots, suggesting such curls as are produced by hairdressers and pigs' tails! In these experiments the clinostat was not employed, there was no motion which might "dizzy" the plant or any of its parts, the stimulus was unchanging in direction as well as otherwise, and the response was continuous and uniform. These experiments, therefore, are also beside the point raised above, but they are of fundamental importance as indicating that the influence of gravity is continuous.

There remain Fitting's experiments, but one need only recall the so-called aviation tests now employed by aurists, to recognize that the use of an intermittent clinostat, in which the position of the plant on a horizontal axis was reversed as frequently as every twelve minutes, is essentially the same as continuous movement. It is obvious that if the rate were once in every thirty minutes or longer, or perhaps even fifteen minutes, the plant would have begun visibly to turn up from its horizontal position before it was turned upside down: but turning it upside down with any frequency within the time in which visible reaction appears (the so-called reaction time) makes of the continuing stimulus a continuous irritant, one effect of which may well be not only the reversing of reactions already begun, but also actual inability to give the usual response.

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[31] Küster, E., *Pathologische Pflanzenanatomie.* 2te Aufl. p. 206, 276+, 1916.

At all events I know of no decisive experiments as yet. One must observe certain precautions in experimenting and one must consider certain unavoidable elements of the experiments. Gravity cannot be excluded, increased, or decreased, and whenever it is opposed some only of its effects are offset, not all. Turning or bending may be forcibly prevented,[32] but the results of continued stimulation and prevented bending are to be seen in anatomical differences from stems and branches of normal experience. If Elfving's or Fitting's experiments on continuous or intermittent clinostats were continued as long as Bücher's, there would be anatomical results which would throw a certain amount of light on the question.

There are certain growth phenomena known as epinasty and hyponasty which disclose the directive influence of gravity. In organs in which, like leaves, there is obvious dorsiventrality, in others in which it is not apparent as form or structure, but is evident in position (horizontal branches), and in organs which are structurally radial but behave as if they were dorsiventral (underground stems), position, and the growth by which position is attained, are conceived to be entirely the results of inner correlations (see pages 258, 291) or of external stimuli. Of these last gravity and light (see pages 296–329) are predominant. There is, however, no distinction implied in the latter from the tropisms previously discussed, yet the word nasty, with prefix epi or hypo, was proposed to indicate unequal growths of the upper or lower sides of such dorsi-ventral organs as leaves, resulting in the downward or upward bendings, respectively, of the leaves, quite independently of the stimulus of gravity or of light. Extended experiment has shown, however, as one might expect, that since no organ can escape the influence of gravity, the nasties are not in fact distinguishable from tropisms.[33] (See page 260 for further discussion.)

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[32] Bücher, H., Anatomische Veränderungen bei gewaltsamer Krümmung und geotropischer Induktion. *Jahrb. f. w. Bot.*, 43, 1906.

The growth phenomena in which the direction of growth is determined by gravity, to which most attention has hitherto been given, and to which a bulky literature is devoted, are those of the primary root and its branches. The ease with which seedlings can be cultivated through the early stages following germination, the considerable growth made by the root immediately after the seed germinates and before the stem or other complications appear, and the fact that the behavior of the root attracted the attention of no less a personage than Charles Darwin, have given this feature of root growth a singularly disproportioned importance. Long after the one significant fact was established that gravity determines the direction of growth of normal primary roots, as it does the posture of man and other animals, and that it is one of the factors determining the growth of their branches, time, thought, and labor were given to studying the relations of roots to this constant, uniform, inescapable force, and to the development of a technical vocabulary of precision quite exceeding the behavior of living things and quite failing to imply their plasticity and diversity.

The fact that the direction of growth of root and stem is determined by gravity was demonstrated by employing the various means of opposing gravity. When gravity is opposed by greater force the growth of the root follows the greater force (Knight's centrifugal experiments). When the growth of the root is opposed by hard or dense material, such as soil or quicksilver, it is delayed or deflected accordingly. When its position is fixed horizontally but the rest of the plant is free to move, the rest of the plant is carried upward (F. Darwin's experiment). And when the plant is slowly rotated on a horizontal axis to which root and stem are parallel, so that neither side is up or down for more than a few moments at a time, growth continues and in opposite directions, but parallel with the axis of rotation.

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[33] Rawitscher, F., Epinastie und Geotropismus. *Zeitschr. f. Bot.*, 15, 65, 1923.

Darwin concluded from his and his son Francis's extensive and ingenious experiments together [34] that the tip of the root is the part sensitive to gravity, and that the region of growth in length, in the four millimeters directly back of the tip, is the part in which the response to the stimulus is executed. This implies the transmission of the *stimulus* or *impulse* from the *receptive* or *perceptive* to the *reacting* region, across a more or less *inactive* zone, during the *time* which intervenes between the exposure to the stimulus and the visible response or reaction thereto, an interval known as the *latent period,* but in which may be included not only the time of transmission of the impulse, but also the time requisite to the development or accumulation of force sufficient to accomplish the reaction. For the reception of sufficient stimulus to be followed by a given reaction there must also be sufficient *presentation time.* All of these have now been determined with great apparent exactness for different species, as may be learned by reference to the literature.[35]

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[34] Darwin, C. and F., *The Power of Movement in Plants.* London, 1880.

[35] Benecke, W., and Jost, L., *Pflanzenphysiologie,* 4te Aufl., Bd 2, p. 251, 1923.

Darwin's conclusion that the tip is the region of the root sensitive to gravity was based in part on faulty experiments, to which Sachs and his school did not fail to take exception.[36] About Darwin's conclusion there was argument, continued till after Czapek, in Pfeffer's laboratory,[37] applying to the tip of the root a short glass tube bent at a right angle showed that, if the tip were vertical, no bending took place in the part behind, while, if the tip were horizontal, the growing part behind would bend, no matter what the position of the shaft of the root.[38] It is objected to this method that the glass tube prevents due exchange of gases, oxygen and carbon dioxide, in the metabolism of the cells at the root tip. While the objection is valid, it should be remarked that, if the glass tubes and the duration of the experiments be shortened to the utmost, gas exchange and metabolism can hardly be interfered with much more than in close grained soil, in which, nevertheless, roots may behave quite naturally. Furthermore, it has been shown by Němec[39] and Haberlandt[40] that, while the presence of free oxygen may be necessary for normal response to stimuli,[41] the response in roots appears to be primarily dependent upon the presence in the cells of the tip of solid particles, starch grains, which act as statoliths. These are present in glass-encased root tips as in others, and will necessarily fall or press downward in response to the pull of gravity. We may, therefore, conclude that the root, sensitive to gravity, perceives the attraction or stimulus with sensitive tip, in the living cells of which there are, as Noll [42] argued and predicted would be the case and F. Darwin [43] confirmed subsequently, starch grains acting as equilibrators or statoliths, and that sufficient exposure results in the transmission of an impulse to the cells of the growing region which so react that the root grows vertically downward.

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[36] Detlefsen, E., Ueber die von Ch. Darwin behauptete Gehirnfunction der Wurzelspitzen. *Arb. d. bot. Inst. Würzburg*, 2, 1878–82.

[37] Czapek, F., Untersuchungen über Geotropismus. *Jahrb. f. w. Bot.*, 27, 1895. Ueber den Nachweiss der geotropischen Sensibilität der Wurzelspitze. *Jahrb. f. w. Bot.*, 39, 1900.

[38] But Newcombe (*Beihefte z. bot. Centralbl.*, 25, 1908) shows that sensitiveness, though greater in the terminal 2mm, is not confined to them.

[39] Němec, B., Ueber die Art der Wahrnehmung des Schwerkraftreizes bei den Pflanzen. *Ber. d. d. bot. Geselschaft*, 18, 1900, p. 241.

[40] Haberlandt, G., Ueber die Perception des geotropischen Reizes. *Ibid.*, p. 261.

[41] Correns, C., Ueber die Abhängigkeit der Reizerscheinungen höherer Pflanzen von der Gegenwart freien Sauerstoffes. *Flora*, 75, 1892.

The phenomenon thus described is known as Geotropism. Roots are positively geotropic, stems negatively so; the branches of roots and stems are said to be plagiotropic or diageotropic, occupying a position between the verticals. The tips of lateral roots, like those of the primary or tap root, are sensitive to gravity,[44] but the growing region does not bend, carrying the tip downwards, so long as the tap-root is intact and living. The same is true of the branches of ordinary erect stems: they too continue to grow plagiotropically unless the tip of the stem is injured. The branches of prostrate stems, on the other hand, presumably bear the same relation to gravity that the main stems do. They are all in effect plagiotropic. But the branches of erect orthotropic stems and of main roots, while also plagiotropic, are so only while the orthotropic stem and the root are intact. When amputation, serious wounding, or other misfortune eliminates stem or root, one or more branches cease to be plagiotropic, become negatively or positively geotropic respectively, and attempt to fill the place of the lost or injured member. This phenomenon, often witnessed on the edge of the forest after heavy wind or near streams after spring freshets, and easily reproduced in the laboratory,[45] implies *first* that the part itself bears a definite relation to gravity (it is "*attuned*" in a certain way to gravity), *second* that this relation may change, and *third* that it and its behavior are correlated to the main stem or main root. Root, stem, and their branches behave as parts of a whole, their behavior is the product of the behavior, the mutual influence, and the experience of all the parts or members of the whole body. This does not surprise us in an animal; it is no less real in a plant. But the means of correlation are different in the two sets of organisms.

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[42] Noll, F., Beitrag zur Kenntniss der physikalischen Vorgänge welche den Reizkrümmungen zu Grunde liegen. *Arb. d. bot. Inst. Würzburg*, 3, 1884–88.

[43] Darwin, F., On the perception of the force of gravity by plants. *Nature*, 70, 1904.

[44] Lundegårdh, Henrik, Die Ursachen der Plagiotropie und die Reizbewegungen der Nebenwurzeln. *Lunds Univers. Arsskrift.* N. F., Avd. 2. Bd. 13, 1917, und Bd. 15, 1919. Das geotropische Verhalten der Seitensprosse. *Ibid.*, Bd. 14, 1918.

Apparently the latest, most thorough, and most critical study of geotropism is the one by Lundegårdh. While more particularly devoted to the behavior of the branches of roots and stems, it may fairly be said to complete, at least for the time, and from the physical as distinct from the chemical standpoint, our knowledge of the relations of roots and stems to gravity, as a directive stimulus. We may advantageously discuss some of its conclusions. They apply also to certain other questions already discussed (see page 253).

To begin with, all roots and stems appear to be sensitive to gravity, the roots ordinarily reacting positively by growing downwards, the stems negatively by growing upward. Such reactions follow, however, only when a given *amount* (so-called) of *stimulus* has been received. Since gravity is a constant, uniform, unchanging force, the quantity of stimulus can most simply be expressed in units of time. We have, then, as the complement of the idea of *quantity of stimulus*, the conception of *duration of stimulus*. The time required to insure the application of enough stimulus to be followed by a complete visible reaction is known as the *presentation time*. The presentation time will vary with the position of the organ, as well as with temperature and the other conditions of existence. A primary root, therefore, lying horizontal is in the position of maximum stimulus and of minimum presentation time. Within a period of time characteristic of the species, under the prevailing conditions of temperature, etc., the root will bend downward. During the *reaction time* the stimulus has been transmitted from the receptive to the reactive region, and the latter has developed the necessary mechanical force to overcome the resistance of organ and environment and to accomplish the bending of a solid cylindrical mass. The quantity of bending will be proportioned to the quantity of stimulus, the speed of bending being controlled by the size and other features of the root itself. Thus Lundegårdh asserts that the primary root of the "pure line" peas with which he did most of his work requires a presentation time of about five minutes, the lateral roots about twelve minutes; while the reaction time of the primary root is fifty-six minutes, that of the laterals is thirty to forty minutes. He finds further, in confirmation of previous work by Fräulein Riss [46] that gravity not only stimulates bending but also the development of a longitudinal force which, while not influencing the perception, does finally neutralize the power of reaction to the stimulus. As shown by motion-picture photographs, the bending of tap and lateral roots in response to gravity is completed through a series of more or less wavering motions. In the living cells gravity induces opposite reactions. In roots the reaction of bending downward predominates; in both roots and stems, in both lateral roots and in branches of stems, bending ceases when these two opposite reactions become equal. The reactions of roots and stems of plants rotated on clinostats are profoundly affected by this experience, the more continued the rotation, the more pronounced the inability of the plant and its parts to react to gravity. From this it becomes evident that epinasty, and conversely hyponasty, (pages 253–254) are fundamentally geotropic phenomena, induced by external influence, and not, as Jost[47] would have it, reactions determined by the plant itself and confined to dorsiventral organs. (As to radial and dorsiventral structures, see pages 315–317.)

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[45] See Ganong, W. F., *A Laboratory Course in Plant Physiology.* New York, 1908.

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[46] Riss, M., Ueber den Einfluss allseitig und in der längsrichtung wirkender Schwerkraft auf Wurzeln. *Jahrb. f. w. Bot.*, 53, 1913.

The directive influence of gravity thus described contributes to the same result as what we considered previously under the term the formative influence of gravity. Every living organism, and every living organ, is inescapably acted upon by mass attraction, its development, its movements, and all other features of its behavior being influenced thereby.

There has recently appeared a careful study and thoughtful statement by Newcombe[48] of the reversal of geotropic response claimed by Small[49] and his associates as taking place in response to certain treatments applied to stems and roots. There is nothing inherently improbable in the idea that the normal response may be replaced by an abnormal one in consequence of sufficient change in circumstances; but Newcombe's experiments seem to show that what have been claimed as abnormal responses to the stimulus of gravity are rather the normal results of injury produced by poisons (acids or alkalis), or by exclusion of oxygen, or by loss of water and therefore of turgor. This would seem also to dispose more or less automatically of the theory of geotropism advanced by Small, throwing us back to the perplexity already indicated (page 248) as to why the same stimulus should awaken opposite response in the head and feet of adult man and in the stems and roots of most plants.

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[47] Jost, L., *Pflanzenphysiologie,* 4te Aufl., Bd. 2, p. 362, 1923.

[48] Newcombe, F. C., The Supposed Reversal of Geotropic Response. *New Phytologist,* 22, 1923.

[49] Small, J., Small and Rea, Small and Lynn, M. J. Lynn, and R. Snow, in the *New Phytologist,* 19 and 20, 1920–1921.

The Influence of Contact

So many different ideas are suggested by the word contact that one should recognize one's meaning before discussing its influence. The human mind is informed by the sense of touch. We learn through it the hardness or softness, the roughness or smoothness of an object, whether it is solid, liquid, or gaseous, whether it is sticky (viscous) or slippery (oily), whether it is still or in motion, whether following impact it presses more or less heavily: but in addition to these qualities of the object one may learn whether it is hot or cold, whether it is a good or bad conductor of heat and even perhaps of electricity. Impact, pressure, friction, and adhesion, besides changes of temperature and electrical potential, are all possible through contact. Through contact, therefore, the unwalled, one-celled, naked mass of protoplasm, whether of plant or animal, as well as the multicellular organism, may be influenced as to its behavior both as to form and size as well as in direction of growth and movement. We may, therefore, in discussing contact, distinguish between its formative and its directive influence.

The means of attachment — holdfasts of various sorts — of the sessile fresh water and marine algæ are examples of the formative influence of contact. The fresh water algæ *Œdogonium* and *Cladophora* from zoöspores, naked one-celled motile masses of protoplasm, which attach themselves to suitable objects with which they come into contact through swimming. Experiment [50] has shown that whether they attach themselves or not, and the strength of their attachment, depend upon the character of the object, apparently mainly the roughness of the surface, with which they come into contact. Thus, when one hangs in a vessel of water containing zoöspores of these algæ some perfectly clean smooth cover-glasses, others coated with gelatine, and still others with ground surface, the zoöspores will not attach themselves to the gelatine-coated glass, or if they do, they form only hypha-like tubes, no holdfasts; on the clean smooth glass they fasten but do not make strong holdfasts; on the ground glass they attach themselves by thoroughly developed holdfasts.

Roughness of the substratum, and the friction due to the movement of the water as well as to the locomotion of the zoöspores themselves, seem to be the main factors in these cases of contact stimulus. This is still further indicated by the behavior of those species of *Spirogyra* which attach themselves by forming rhizoids.[51] On the lime-encrusted boards of watering troughs in this region one may find *Spirogyra* living attached by hypha-like processes or branches forming more or less pronounced holdfasts at the end. The slow movement of the water rubs the filaments of *Spirogyra* against the rough surface and a hypha-like branch, formed at the point of contact or friction, attaches itself to the support. On gelatine they make no attachments.

Experiment [51] with the non-motile spores of certain marine algæ shows that they behave similarly to the zoöspores of *Œdogonium* and *Cladophora*. Contact with a more or less rough surface is followed by a correspondingly firm attachment. In our cultures, and in many places in nature, the conditions are such that gentle rubbing of the naked protoplasm against the rough object can be followed in due time by the formation of a holdfast; but on rocky coasts exposed to the full violence of the open sea the algal vegetation may be very rich. The time between waves during which the microscopic masses of protoplasm, which constitute the one-celled spores of these plants, can attach themselves to the rocks must be very brief indeed. I have long marveled at the sea palms (*Postelsia palmæformis*) living on the most exposed ledges of the rocky coasts of California, forming massive holdfasts which fasten these large erect brown seaweeds to the sloping surfaces on which the surf pounds and thunders and over which the waves surge backward and forward with almost irresistible power. Between times the one-celled motile spores of *Postelsia* must fall or be carried against the rough rock and attach themselves to the surface, so firmly as not to be torn loose by the next wave. How can this attachment be effected if it is merely a matter of friction and subsequent growth?

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[50] Peirce, G. J., and Randolph, Flora A., Studies of Irritability in Algæ. *Bot. Gazette,* 40, 1905.

[51] Peirce and Randolph, *loc. cit.*

As already indicated (page 15), protoplasm is a system consisting of colloids, electrolytes, fats, and water, on the interfaces of which and on the outer surface of which are tensions and forces which unite these diverse elements into mechanical, physiological units, the coherence of which as self-operating mechanisms under a great variety of conditions is most remarkable. A one-celled naked mass of protoplasm is held together by these surface forces in the water in which it is suspended and in which it does not diffuse. The rock is another system, consisting of electrolytes and water, also with surface forces. If one can conceive these two systems, the protoplasm and the rock, instantly being held together when they touch by these powerful surface (electrical and other) forces, one can conceive how these one-celled spores can be held upon these ledges firmly enough to resist the tremendous wave action. At best the mortality among these spores must be very high. The wonder is that it is not total.

The hypothesis thus suggested is strengthened by observation of many of the sea-anemones living on granitic rock. These protoplasmic masses are often so covered with grains of sand that they present the same appearance as the rock on which they are living. As the grains of sand fall or drift over them, they stick. The sand does not stick indiscriminately on the surfaces of animals and plants. Gelatinous and other smooth surfaces do not hold it. The red marine alga *Iridea* and the notoriously slippery freshwater alga *Spirogyra* are strikingly free from all lodgers. Their exceedingly smooth gelatinous surfaces offer no hold to spores or other foreign bodies. But may one not suspect that between the gelatinous surface and the sand, and between the gelatine covered surface and the spore, there may not be such oppositeness or appositeness of surface forces as will enable them to unite? On the other hand, between rock and naked protoplasm there may be such, and a union may result, not by reason of irritable reaction but in consequence merely of the instantaneous establishment by contact of a physical-chemical condition resisting great destructive mechanical force by great coherent force.

This hypothesis, applying directly to spores and perhaps other naked masses of protoplasm, may indeed furnish the basis for an understanding of the influence of contact on cells enclosed by cell walls. Pfeffer's observation[52] that liquids and moist gelatine do not irritate by mere contact may well be based, not on the condition of liquidity or solidity, but rather on the condition of the surface of the liquid or wet solid. The question thus raised deserves thorough investigation in the light of what physical-chemistry has shown us since Pfeffer's investigations led to the conclusions current for forty years.

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[52] Pfeffer, W., Zur Kenntniss der Kontaktreize. *Unters. a. d. bot. Inst. Tübingen,* Bd. 1, 1885.

The influence of irritation by contact with a rough surface is shown, further, by the tendrils of the so-called Boston Ivy (*Ampelopsis Veitchii*). These branched organs bear at their tips small cushions which remain small unless they come into contact with brick, stone, or plaster walls, rough wood or paint, whereupon they flatten themselves against the solid surface, forming holdfasts or feet which grow to several times the size of the unstimulated tips. Experiment[53] shows that it is contact with the rough surface which causes this development. The development of the mechanical tissues throughout the length of the attached tendril is due to the increasing strain, and this is plainly a consequence of gravity (page 242).

The formation of haustoria by dodder (*Cuscuta*) and by some of the fungi (*Mucor*) has been attributed to the stimulus of contact.[54] So far as dodder is concerned the case seems to be established, but the complete development of the haustoria follows only when they form in contact with a support which is nutritious and which contains no injurious substance. Thus they may begin on glass, though not on glass coated with wet gelatine, but they will not develop completely unless they are in contact with a living support of suitable size and shape, and quite harmless (not *Euphorbia*, for example). This has apparently been overlooked by Gertz,[55] who attempted to induce the formation of haustoria on all sides of the dodder simultaneously by establishing stimulating contact all the way round. Another source of difficulty in his incompletely successful experiments is his ignoring of the relation of the dodder stem to gravity, for like other twining plants it does not twine about horizontal supports, however suitable in size and substance (see Peirce[54]). Similarly, the formation of rhizoids by fungi, whether saprophytic like *Mucor*, or parasitic like those in lichens,[56] may be due to contact stimulation; but there is no reason to question that their complete development is due in large part to the chemical stimulation of the nutritious material upon or around which they grow.

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[53] Fitting, H., Untersuchung der Haptotropismus der Ranken. *Jahrb. f. w. Bot.*, 38, 1903. Weitere Untersuchungen zur Physiologie der Ranken. *Ibid.*, 39, 1903.

[54] Peirce, G. J., A Contribution to the Physiology of the Genus Cuscuta. *Annals of Botany*, 8, 1894. Wortmann, J., Ein Beitrag zur Biologie der Mucorineen. *Bot. Zeitung*, 39. 1881.

[55] Gertz, O., Untersuchungen über die Haustorienbildung bei Cuscuta. *Centralbl. f. Bakteriologie.* Abth. II, 51, 1920.

The influence of contact on locomotion must also be taken into account. As previously indicated (page 248), locomotion in plants and animals is possible only when the action of gravity is sufficiently opposed by the substratum; but a substratum of sufficient solidity and roughness is required by us as a condition of walking. The nature of the surface of the substratum with which we are in contact is one of the factors determining the direction of our locomotion. This is equally true of certain motile plants, of which *Oscillatoria* and many diatoms may be mentioned as examples. In these instances, however, the influence of the direction and intensity of light are so much more striking that the influence of contact is obscured. One may notice, however, that *Oscillatoria* moves along the line of contact between the bottom or sides of the glass or pottery vessel and of the water in which it is living, or along the line of contact of the water with the air, not swimming in the layers between. It seems to be, in these instances, not so much a matter of contact with a solid object as with a different physical system. Both at the top and at the bottom of the water, the water forms a surface film, denser, more firmly held together, than the rest. It is along this film, at the top or at the bottom, that *Oscillatoria* moves. Motile diatoms, on the other hand, swim freely in the water, though they may be caught in the surface films.

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[56] Peirce, G. J., The Nature of the Association of Alga and Fungus in Lichens. *Proc. Cal. Acad. Sci.*, 3d Ser., Botany, 1, 1899. The Relation of Fungus and Alga in Lichens. *Amer. Naturalist*, 34, 1900.

The classical objects for showing the influence of contact in plants are tendrils, but the petioles of the leaves of certain plants (*e.g.*, *Solanum jasminoides*) and the stems of the curious twining parasite dodder also exhibit it. Whether ordinary roots are sensitive to contact has long been disputed, without evident reason, but the roots formed on the stems of English Ivy (*Hedera helix*), attaching it to its supports (walls, trees, etc.), may well be, in part at least, the product of contact stimulation. If ordinary roots are sensitive to contact with solid objects, then their habitat, the soil, must subject them on all sides and constantly to a confusing contradictory succession of contact stimuli. Nevertheless, the dictum of Sachs,[57] great but not infallible, was all that was needed to include roots in the category of plant organs sensitive to contact. The experimental demonstration by Newcombe[58] that Sachs had been misled to an erroneous conclusion by the chemically irritating nature of the materials with which he had experimented, disposes of the matter consistently with reason. We should not regard ordinary roots as possessing contact irritability.

While there are many leaf stalks as sensitive as some kinds of tendrils there are none which exhibit the extreme sensitiveness and prompt response of the most sensitive tendrils.

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[57] Sachs, J. von, Ueber das Wachsthum der Haupt- und Nebenwurzeln. *Arb. a. d. bot. Inst. Würzburg,* I, 1872.

[58] Newcombe, F. C., Sachs' angebliche thigmotropische Kurven an Wurzeln waren traumatisch. *Beihefte z. bot. Centralbl.,* 12, 1902.

These latter have been subjected to earnest study for many years with the result, among others, that a technical vocabulary has been developed also. Thigmotropism, stigmatropism, stereotropism, haptotropism, are synonyms for the phenomenon displayed by tendrils and other organs in consequence of the stimulation produced by contact with certain objects. In these multicellular organs, the cells are enclosed in cellulose and other walls. There is, therefore, no direct contact of protoplasm and foreign object, as in the germinating zoöspore. Furthermore, the point of contact is not the only part which reacts. There is a transmission of stimulus from cell to cell. This, and the development of enough mechanical force to effect the bending of a solid turgid mass of cells, take time to accomplish. Nevertheless, the promptness with which bending follows contact, when conditions favor, is astonishing. This can be best comprehended if we describe the phenomenon as it takes place in certain well known or easily available plants.

The classical example for tendril studies is the passion vine (*Passiflora*), but the wild cucumber of the far west (*Echinocystis*) is equally sensitive. The tendrils of these plants are long, slender, almost whip or fishing-rod-like structures, self supporting from the base but easily bent, more or less round in cross section, and slightly tapering. The structure shows the usual supply of vascular and mechanical tissue (fibers), with chlorophyll-containing parenchyma, covered by rather thin-walled epidermal cells. Tendrils, whether of these particularly sensitive species or of the much less responsive grape, pea, etc., grow in length at extraordinarily rapid rates. They may double their length in twenty-four hours, but within a week they are through growing. Unlike root and stem their growth is distributed throughout their length (intercallary). Before they are half grown they are comparatively unsensitive; from then on for several days they may be extremely sensitive, but their sensitiveness is profoundly affected by precisely those factors of the environment which influence life in general, more especially warmth and moisture of air and soil. If, having fully grown in length, a tendril does not successfully twine about a support, it will begin to grow again, but unequally so that one side becomes convex, the opposite concave, and what are known as spontaneous coils are made, after which the tendril ceases to have any possibility of usefulness to the plant and may dry and die. During its period of very rapid growth the growth is not equal on all sides and the tip of the tendril is pushed in various directions, generally in orderly sequence, so that, by this circummutation as Darwin called it,[59] the tendril explores all parts of its environs.

If in its course the tendril touch an object suitable in size, shape, and surface, the part beyond the point of contact toward the tip will bend toward the object, thus increasing the contact and thereby increasing the stimulus, which is followed by continued bending. If it is a stationary object which the tendril has touched, it will bend around the object once or twice or even thrice, forming spiral turns about it, and thus completely enclosing it, as a sailor's rope is wound about a pile when he "makes fast." Experiment and observation show that, within a very few seconds after contact, bending visibly begins, to continue in speed and extent directly in proportion to the duration and intensity of the contact stimulus.

Pfeffer's study of tendrils[60] remains the most original and the most informing of the many that have been carried on between Darwin's pioneering investigations[59] and Fitting's com-

[59] Darwin, C., assisted by F. Darwin, *Movements and Habits of Climbing Plants,* 2 ed. New York, 1876.

[60] Pfeffer, W., Zur Kenntniss der Contaktreize. *Unters. a. d. bot. Inst. Tübingen,* Bd. 1, 1881–5.

paratively recent ones.[61] From Pfeffer we learn that the bending is due to accelerated growth on the side opposite the point of contact, from Fitting that growth is accelerated on both sides but more on the untouched side. There seems to be little or no turgor change in any tissue, but the suddenly increased rate of growth in an already very rapidly growing organ is remarkable. To induce visible bending of a tendril of *Passiflora* an extraordinarily slight stimulus is necessary, such, for example, as the weight of a fiber of cotton weighing 0.00025 mg, provided this is kept lightly rocking by a breeze. Pfeffer showed in addition that liquids and moist gelatine, even when the contact is brought about by pronounced impact, do not stimulate. Rain drops may strike, but they do not cause tendrils to coil. Most moist objects, however, are as stimulating as dry objects of equally rough surface. Pfeffer's conception of the stimulus is, then, that of pressure or pull (from adhesion) exercised upon separate points close together, rather than of uniform pressure or pull over a continuous area. Brief contact of this sort induces temporary bending, after which the tendril gradually resumes its natural curvature; continuing contact correspondingly induces continuing bending, with permanent results.

While pressure or pull can readily be imagined to exercise such irritation as will stimulate growth, the briefness or lightness of contact required to produce visible reaction, and the promptness and swiftness of the reaction, are so extraordinary that one has difficulty in conceiving the manner of transmitting from cell to cell any such purely mechanical impression and the means of reacting to it by such a complex of processes as those comprehended under the term growth. As animal physiologists are still struggling to determine the nature of the nerve impulse and to ascertain the essential features of the actual stimuli,[62] so plant physiologists have penetrated perhaps even less to the heart of the questions involved in stimulus and response. In the case of contact stimulation, however, whether the stimulus be that effected between a rough object and a naked mass of protoplasm, or between a rough material and living cells enclosed by cell walls, there must be more than pressure or pull resulting from contact; there will be changes in the balance of electrical charges, there may well be other changes of balance, *throughout the system*, and these changes will be *instantaneous*. Thus the hypothesis advanced in regard to contact stimulation of naked protoplasm (page 263) is extended to tendrils and other organs composed of cells enclosed by cellulose or other walls or membranes; but it is advanced as a working hypothesis, a suggestion for investigation, not as dogma.

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[61] Fitting, H., Untersuchungen über den Haptotropismus der Ranken. *Jahrb. f. w. Bot.*, 38 und 39, 1902–3, 1904.

In this connection the behavior of the rest of a tendril which has wound itself about a permanent support may be discussed. The contact which is followed by still more rapid growth of the side opposite the point of contact is followed by an increased rate of growth along the same side toward the base also. Such unbalanced growth must obviously result in bending the part of the tendril which passes through the air, as we have seen it does in the part in contact with a support. This bending will quickly fall into a spiral, but a spiral attached at both ends must soon cease to grow, or must be twisted loose from base or tip, or must be opposite and equal in two or more regions, with a neutral point or points between. This last is precisely the development which takes place. If one examine *Passiflora*, *Echinocystis*, or *Vitis* tendrils, out-of-doors or in, one will see that the plant is pulled toward its support, and is held as on coiled spiral springs, by the tendrils which have twined about their supports, coiled between stem and support, and dried to wire-like toughness and elasticity. These spiral springs are compound, with one or more neutral points between parts oppositely coiling. By what mechanism are these neutral points and these reversals of direction of coiling accomplished? Nothing further is known about this than that it seems to be a product of the same stimulus which is followed by the coiling about a support.

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[62] See Bayliss, *loc. cit.*, 4th ed., 398, 1924.

Throughout the tendril thus stimulated, and thus responding, there is a rapid development of the mechanically strengthening tissues. This is indicated in part by enlargement of the base of the tendril and other increases in thickness: but anatomical and microchemical investigation shows that cell walls are thickened and hardened also. These developments, while following contact irritation in time, are not caused or induced by it, but are a reaction to strain entirely similar to those previously examined (pages 239–245).

The principles indicated in this discussion of the behavior of tendrils apply equally well to the phenomenon of sensitiveness to contact displayed by such leaf stalks as those of the potato vine (*Solanum jasminoides*) and by the stems of dodder (*Cuscuta.*) They do not apply to most twining plants; for in these plants the twining habit is not a consequence of contact stimulus but of such a combination of long slender form, comparative mechanical weakness, rapid growth on all sides successively rather than simultaneously, with consequent ample circummutation, the complex being controlled by a sensitiveness to gravity which keeps the stem orthotropic. Some twining plants wind upward and around their supports, twining in the direction of the hands of a watch, others counter clockwise. If scarlet runner (*Phaseolus multiflorus*) seedlings, for example, are grown in separate pots on the turntables of a multiple clinostat[63] which rotates alternating seedlings clockwise and counter clockwise on vertical axes simultaneously and under identical conditions, it will be seen that those seedlings rotated contrary to their direction of nutation do not twine about the sticks used for support, but grow orthotropically upwards, as far as their comparative mechanical weakness permits. The seedlings rotating on the turntables consistently with their direction of nutation twine rather more closely than those not rotated at all. Although the mechanics of twining have been studied to the point of exhaustion, as shown by the literature,[64] the problem is not clearly solved, and I leave it with this observation complicating it still further.

In the same unsatisfactory state is the question as to how the appearance known as torsions which is exhibited by many twining plants is developed in them and in trees, shrubs, and other plants as well. Great trees of the forest or in the open on the High Sierra, junipers, firs, and pines, are shown by lightning to have trunks the grain of which runs spirally, not vertically, upward. The course of the lightning bolt is often exactly the course of the torsion. In trees of the same species growing side by side, though not necessarily close together, the torsions may be opposite. Anatomical studies, together with a knowledge of rainfall and other climatic conditions prevailing during the successive growing seasons, will no doubt throw light on this problem, with which contact stimulation has nothing whatever to do.

There are many examples of sensitiveness to contact which belong in entirely different categories from those now discussed. Some of these are similar to the purely mechanical sensitiveness of a trigger which, when touched, springs forward in response to tension. The stamens of mountain laurel (*Kalmia latifolia*) are of this sort. The stamens of various species of barberry (*Berberis*) and of certain of the *Compositæ* move very rapidly in response to touch, but the movement is not a sudden snap such as results from the release of a spring or bow under tension, but rather a quick release which may be due to a decrease in turgor (water pressure).

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[63] Peirce, G. J., Ein multipler Klinostat. Pfeffer Festschnift. *Jahrb. f. w. Bot.*, 56, 1915.

[64] Gradmann, H., Die Bewegungen der Windepflanzen. *Zeitschr. f. Bot.*, 13, 1921.

The careful studies of Newcombe[65] both in the greenhouses of the University of Michigan and out-of-doors on the campus of Stanford University and on that of the University of Hawaii, add much to our knowledge of the behavior of stigmas which close in response to contact. Besides, Newcombe plainly indicates the advantage to the plant in such singular behavior. He shows that "it is idle to attempt to bring all species under a single rule of action" and points out that too little attention has been paid to the conditions of the habitats of the different plants and the capacity of pollen for self-fertilization. The stigmas of one plant (*Spathodea campanulata*) will close only when pollen is applied with pressure, neither the pollen alone nor the pressure alone being able to do more than start a closing of the stigmas. In this instance pressure (contact) and chemical stimulation, in the form of both water withdrawal for germination and also the excretion of some presumably injurious substance by the pollen grains, are required to bring about complete and permanent closing of the stigma. Between the closed lobes of the moist stigma the pollen germinates freely, much better than on the open stigma even in the moist warm air of Honolulu. The stigmas of *Tecoma stans*, of the calabash tree

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[65] Newcombe, F. C., Significance of the Behavior of Sensitive Stigmas. I, *Amer. Journ. Bot.*, 9, 1922. II, *ibid.*, 11, 1924.

(*Crescentia cujete*), sticky monkey (*Diplacus glutinosus*) and many others listed by Newcombe, close on contact only, quite apart from the nature of the object touching the stigmatic surface. The open stigmas of *Diplacus* begin visibly to close immediately after being lightly touched with a pencil point or other small not sharp or chemically active object: but the reaction is immediate only when conditions are favorable, that is, when the air is warm and not too dry, the sun is shining, the plant has sufficient moisture in the soil, and is not roughly shaken by hard drying winds. These are conditions prevailing in this vicinity in spring. Any departure from these optimum conditions entails slower reaction. The mechanism of reaction in this plant is a reduction in turgor of the tissues of the upper parts of the stigmatic lobes.

The discharge of water from the turgescent cells of cortical parenchyma into its intercellular spaces and into the vessels of the wood of the vascular bundles appears to be the means of bringing about the closing of the leaflets and the drooping of the leaves in the best known of all the plants sensitive to contact, *Mimosa pudica*, "the sensitive plant." This singular plant responds, however, not only to contact by closing its leaflets, but also to jar, chemical irritation, electric stimulus, heat, and darkness. It is a tropical and semitropical legume, commonly cultivated from the seed in greenhouses, etc., and more or less established in the southern states. The leaves are compound and further complicated by the possession of three sets of joints or pulvini. The petiole of the whole leaf has a simple large pulvinus at the base, adjoining the branch. Each of the three or four petiolets also has a pulvinus of corresponding size at its base, and each leaflet has a still smaller pulvinus at its base. A pulvinus consists of a central fibrovascular strand, surrounded by cortical parenchyma composed of large thin-walled cells with large central vacuole.

Apparently the lower half of each pulvinus is more sensitive than the upper half, but the sensitiveness to contact is common to the pulvini and the blades of the leaves or leaflets. Furthermore, stimulus by contact at one point may be followed by reaction at another. Stimulus of the lower half of a pulvinus will be followed by discharge of water from its turgid cortical parenchyma cells into the adjacent air spaces, and the drooping of the petiole and its blade. Change of color and increased translucence of the pulvinus are accomplished by this injection of the intercellular spaces owing to the displacement of the air by water. Gentle stimulation of one pulvinus will be followed by response confined to the single system of petiole and blade. More pronounced irritation of the one pulvinus will be followed by the activity of several pulvini and the consequent drooping of the several petiolets of one leaf or the whole of several or many leaves, according to the violence of the disturbance at one spot. The same is true of stimulus applied to the blades of the leaves. The impulse which effects prompt reduction in turgor in one pulvinus may be transmitted to adjacent pulvini of the same or other leaves. In this way shock applied locally may bring about the closing of all the leaflets and the drooping of the leaves of an entire plant.

The measurement of the stimulus of contact, and of some of the other stimuli to which Mimosa reacts, conveys at best little information. Bose[66] and others, using electrical stimulation, have obtained more significant measurements. The skepticism which prevails in this country in relation to the experiments, the methods of experimentation, and the conclusions of this Hindu, who has distinguished himself from his fellow countrymen by his devotion to biological science, may not lack prejudice but is at least partly justified by the adverse ratio between evidence and conclusions. By means of ingenious combinations of clockwork and electrical apparatus Bose has produced autographic records of the behavior of Mimosa under various conditions of environment and of stimulation. Working under climatic, and perhaps other, conditions more favorable than those prevailing in the more northern laboratories of Europe and the United States of America, Bose obtains figures and reaches conclusions some of which seem quite incredible; but just as Newcombe[67] pointed out in his study of irritable stigmas, so in connection with such an exceptionally and strikingly sensitive organism as Mimosa, the conditions under which the plant is living must greatly influence its sensitiveness and power of response. For instance Bose[68] claims to have measured the time elapsing between stimulus and response and to have found it to be eight hundredths of a second! It may well be questioned whether, in this and many other instances, the experimental error does not far exceed the sensitiveness of the organism. By means of what he calls an oscillating-recorder — a glass plate swinging like a pendulum — he secured autographic records of the diurnal variation of the reactions of Mimosa. Inspection of the diagrams of his apparatus and of the records entirely justify the doubt expressed above, although the results are what would in general be expected.

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[66] Bose, J. C., *Comparative Electrophysiology.* London, 1907. *Researches on Irritability in Plants.* London, 1913. *Motor Excitability in Mimosa.* Royal Institution, London, 1914.

As to the mechanism of response, the reduction in turgor of the cortical parenchyma cells of the pulvinus, we have fairly precise measurements in the form of determinations of the electrical conductivity of the cell sap expressed from the wound surface of excised pulvini.[69] Objectionable as Bose's experiments may be on the ground of experimental error, these of Blackman and Paine are horrible since they involve excision, suspension of the amputated pulvinus in a water bath, and the teasing of the wounded organ by various unnatural means. That such vivisection produces twitchings (called autonomous or autogenic contractions) in this plant, similar to those of animals, is recorded by Blackman and Paine.

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[67] *L. c.*, p. 90 *et seq.*

[68] Bose, J. C., An Autographic Method for the Investigation of the Transmission of Excitation in Mimosa. *Philos. Trans. Royal Society.* London, 1913. On diurnal variation of moto-excitability in Mimosa. *Annals of Botany,* 27, 1913.

This observation is very significant. Sounds and struggle are the common signs of protest on the part of the higher animals against torture. The absence of these signs among the lower animals and the plants leads thoughtless persons to infer a lack of sensitiveness on their part. The twitchings of the so-called sensitive plant show, however, that a plant provided with the means of response will indicate its sensitiveness in an evident manner, and that we are entirely unjustified in concluding that there is no " feeling " merely because there is neither sound nor struggle.

Mimosa is one of many plants which execute so-called sleep or nyctitropic movements. These will be discussed in the section devoted to the Influence of Light (pages 296–329). The leaves of certain of the carnivorous plants (pages 116–119) are sensitive to contact, but as their response is primarily to chemical stimulation the phenomena may well be discussed together. The attempt to distinguish Mimosa and similar plants from others sensitive to contact because they close their leaflets in response to jar as well as to touch is of uncertain value. We may content ourselves, therefore, with mentioning the attempt and letting the interested student pursue the subject at will.[70]

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[69] Blackman, V. H., and Paine, S. C., Studies in the permeability of the pulvinus of Mimosa pudica. *Annals of Botany*, 32, 1918.

[70] Jost, L., and Benecke, *l. c.*, II. p. 384.

Influence of Injury

The hazards of life produce injury to which the organism may respond; instead of merely submitting, it may react. The injury and the reaction may be slight or great, according to the severity of the experience. Pressure, distortion, wounding, amputation or dismemberment are terms which may suggest various degrees of experience to which plants are exposed in nature and are subjected in cultivation. That some of these constitute a part of horticultural practice indicates that plants respond or react to them. As in the case of gravity and contact, the plant reacts to injury in ways which indicate that its influence is formative or directive. Man may make use of these reactions for his own purposes, training, distorting, stimulating the production of bloom or fruit, as he wills.

Wounds produced by mechanical means are ordinarily closed even in organs and tissues the component cells of which seem long since to have lost their power of division. Corrosion or other injury due to chemical means is not likely to be as simply and promptly healed. For example, leaves bitten by insects generally heal the wounds by means of the cells immediately adjoining the injured ones, epidermal and cortical parenchyma cells promptly dividing, the outer daughter cell in each case developing into an epidermal or cork-like cell. But if the injury is produced by sulphur dioxide gas, as in certain smelter regions, or by other poisons, the wound dries and may crack instead of closing. In these instances mechanical injury produces a stimulus followed by a healthy reaction, whereas the chemical injury, presumably not confined to the cells visibly hurt, does not stimulate.

More extensive injury, such as that made by amputation of limbs or by burns on the butts of trees, requires much more extensive and active "healing in" than can be accomplished merely by a single division of the whole cells adjacent to the wound and the subsequent differentiation of the outer cell of each pair of daughter cells. In these instances the wound is closed by means of overgrowth centripetally from the uninjured tissues around the margin of the wound. By this means the stump of an amputated limb may be completely covered in, leaving scarcely a scar, in the course of years. The tissue first formed comes from the cortical parenchyma, if there is any, from the living cells of the phloem, and from the cambium. It is called callus. It consists of thin-walled, turgescent, irregular parenchyma cells, among which cork and other definitive tissues differentiate, tending to restore and complete the organization injured or destroyed by the wound.

By means of such overgrowths the scars of forest fires become so closed over as to be completely concealed until lumbering reveals the ancient wounds.[71] Similarly infections, both fungus and phænogamic, may become so closed over that trees may present a perfectly sound appearance but be worthless as lumber.[72] This is particularly true of the Incense Cedar (*Libocedrus*) and its infesting mistletoe (*Phoradendron juniperinum libocedri*). Ancient infections, from which recovery is long since complete, leave lesions which, if numerous, ruin the wood for commercial purposes.

In plants, as well as in animals, the healing of mechanical or other injuries may be delayed or altogether prevented by parasitic infections of the wounds. These it is the province of plant pathology to describe.[73] In horticultural practice the effort to prevent infections of the wounds deliberately made in pruning, trimming, etc., is a recognition of the ability of the plant to react and recover if permitted.

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[71] Dudley, W. R., *The Age of Sequoia.* Dudley Memorial Volume. Stanford University, 1913.

[72] Meinecke, E. P., *Forest Tree Diseases common in California and Nevada.* U. S. Dept. Agric., Forest Service. Washington, 1914.

[73] Sorauer, P., *Handbuch der Pflanzenkrankheiten.*, 3te Aufl., 3 vols. Berlin, 1909–13. Engl. trans. and publ. by F. Dorrance, Washington, 1922 *et seq.*

Certain infections, however, instead of merely keeping a wound open and extending the destruction and necrosis further and further, stimulate the cells and tissues to definite and characteristic reactions. The formation of tubercles in the lung and in other organs attacked by *Bacillus tuberculosis* finds its counterpart in the formation of root tubercles in plants following infection by *Bacillus radicicola*[74]: and just as certain animals are immune to the attack of *Bacillus tuberculosis* and other parasitic organisms causing specific diseases, so most plants are immune to the attack of *Bacillus radicicola* which causes the formation of root tubercles in peas, beans, and other legumes. Various important questions besides the one of reaction to stimulus are raised by this relation of bacteria and higher independent plants. Among these are the whole matter of immunity, natural and acquired, and the material bases of this condition. Into this matter, upon which apparently even more acute effort must be expended than has been hitherto, we cannot go here, however important it is. Immunity is due in certain instances, as is sterility in certain other instances, to anatomical impediments. In others as shown to be the case in the roots of grass seedlings,[75] it is due to the reaction of the invaded organism itself, which cuts off the invader by cell division and the sloughing off of the infected areas. This is plainly a reaction to injury, but mainly chemical injury rather than mechanical.

In the absence of anatomical impediments and of such morphological reactions as just described, hypothesis has not hesitated to invoke such elusive "antibodies" as hormones, antitoxins, etc. Since the specific differences in the behavior of plants rooted in the same soil must have material bases, and as increasing immunity with advancing age cannot depend upon the lapse of time alone, one naturally attributes the result to the chemical composition of the part or the organism, attempting to increase the definiteness of the conception by increasingly precise labels. Thus the words hormones, vitamines, etc., convey ideas, the value of which becomes doubtful only when one fails to recognize that these ideas are as yet hypotheses and not facts. While it is certain that the roots of grass seedlings resist infection by cutting off the tips of root hairs into which *Bacillus radicicola* has penetrated, this abscission may be due to the reaction of the protoplasm of the hair to the "toxin" formed in the hair by the bacteria; or it may follow the production by the protoplasm of a hormone or other antibody or antitoxin which is unfavorable or fatal to the invading bacteria. Experiment alone can reveal the value in plant physiology of such conceptions, introduced from animal pathology and physiology. Throwing a certain amount of light upon the question are the experiments of Robbins,[76] and of Haberlandt,[77] in the former of which amputated root-tips grew in spite of the ordinarily fatal wounding, and in the second of which the presence and movement of a hormone or hormones was suggested by cell divisions which did not occur unless suitable pieces of tissue touched each other. On the other hand, growth in

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[74] Peirce, G. J., The root tubercles of bur clover (Medicago denticulata) and of some other leguminous plants. *Proc. Cal. Acad. Sci.*, 3rd Ser., Bot. 2, 1902.

[75] Peirce, G. J., *loc. cit.*, p. 301.

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[76] Robbins, W. J., and Maneval, W. E., Further Experiments on the Growth of Excised Root-tips under Sterile Conditions. *Bot. Gazette*, 76, 1923.

[77] Haberlandt, G., Uber Zelltheilungshormone und ihre Beziehungen zur Wundheilung, Befruchtung, Parthenogenesis, und Adventivembryonie. *Biol. Zentralbl.*, 42, 1922.

Bryophyllum[78] appears to take place without growth or other hormones being necessarily predicated as parts of the system.

Whether the stimulus or irritation caused by a gall insect is due to the hormones of the leaf or twig, or to the toxins formed by the egg or the larva hatching from it, can be determined only by chemical investigations supplementing the anatomical work that has so far been put upon the subject. Certain it is that further study of this singular form of parasitism promises rewards to the curious, whether interested primarily from theoretical or from practical motives.

The many forms of galls, from those involving serious mechanical injury to those in which apparently the harm is done through contact, may be found described elsewhere.[79] Where no puncture or other wound is produced at oviposition or later, the presence of the egg and the growth of the larva of the gall fly can produce mechanical injury only by pressure. In the Monterey pine, the thickened bases of the needles do not suggest that the shortness of the needles is due to pressure by the larva. Nor does the thickening of the bases of the needles indicate that the needles are robbed of food or injured by a general poison. The galled needles in fact weigh more than normal ones, hypertrophy rather than stunting has occurred, the usual coördination in the growth of the needle has not been attained, the needle is shorter but also thicker than usual. Reinvestigation of the galls by a physiologist chemically minded as well as chemically informed should determine whether enzymes or hormones of these or other sorts diffusing from the infesting larva stimulate or check growth. On a single leaf of white oak (*Quercus lobata*), for example, one may find five or six different shapes of galls. These house the larvæ of as many different species of gall insects. The tissues which form these different galls are all of the same origin in the blade of the leaf, but these mesophyll, epidermal, and vascular cells respond differently to the different irritations or stimuli set up by the deposit of eggs of different species of insects, forming spherical, conical, stellate, erect or depressed galls of different characteristic sizes. The substratum or host is the same — a leaf of *Quercus lobata;* the cause of stimulation is the same — oviposition; time of deposit, the rate of growth, the probable demands for food by the different larvæ are presumably similar; the excreta may be approximately similar; but among these we may imagine growth hormones, characteristic of the individual species of gall insects, and only skillful, open-minded investigation will show whether a starry hormone gives the impulse to the formation of a stellate gall and another hormone to the formation of a conical gall!

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[78] Reed, E., Hypothesis of Formative Stuffs as applied to Bryophyllum calycinum. *Bot. Gazette,* 75, 1923.

[79] Cook, M. I., Galls and insects producing them. *Bulletin Ohio State University,* Ser. 6, No. 15, 7 No. 20, 8 No. 13, 1902–4. Küster, *Die Gallen der Pflanzen.* Leipzig, 1913. Peirce, G. J., Studies on the Monterey Pine. *Bot. Gazette,* 37, 1904.

In all associations of organisms both parties to the association necessarily influence each other, injuriously in many respects, favorably in others. There results from the association of two kinds of organisms a society which has its own character and which appears and behaves strikingly like an individual. In certain instances these societies have been mistaken for individuals. Of these the most familiar, perhaps, is the lichens in which algæ, quite independent and self-nourishing, are associated with fungi, quite incapable of manufacturing their own food. According to the kinds of algæ and of fungi composing them, these societies, villages in a sense, present different characters; but these characters may be classified, and are used to determine what, in individuals, are called families, genera, and species. The anatomy of these arrangements has been abundantly studied,[80] but their physiology is still hardly known. It appears at the present time, however, that one of the consequences of association has been the loss, on the part of the fungus, of those characters distinguishing it from others and incidentally made use of by the taxonomist in classification; and on the part of the alga, of spacial and other freedom, whether ordinarily used or not.

In similar fashion other associations, parasitic, saprophytic, or symbiotic, induce departures, on the part of their components, from the characters or practices of individual separate existence. These departures, while giving to the association its characters as a social unit, are reactions to the favorable or injurious influences mutually exercised by the components. Hypertrophic tissues of various sorts are among the consequences of fungus or bacterial parasites attacking plants, the lower animals, and man. These hypertrophies are more than the results of the abstraction of food from the host by the invading organism; they are probably more than the results of mechanical irritation; they may be the consequences of such chemical stimulation as is suggested by the term hormones; that is, the secretions of the foreign organisms. Such hypertrophies are, for example, caused by the bark-infesting fungus *Peridermium*.[81]

In certain instances morbid growths in plants also have commercial value, comparable to the economic importance of *pâté de foies gras* which, as is well known, is made mainly from hypertrophied goose livers. Redwood burl, birds' eye maple, and similar abnormal woods are prized in cabinet making. These owe their extraordinary "grain" apparently to stimuli, possibly infections, but more probably mechanical injuries due to blows, pressures, or wounds upon young parts or young plants. In these the relatively thin-walled cells, composing tissues of marked elasticity, compose also a larger proportion of the plant or organ than when the part is older. In response to the injury many adventitious buds form. These, failing to develop, become buried in the woody mass in which they form the "birds' eyes" or the centers among which the vascular tissues bend and turn. Fire may also be the cause of the injury which is followed by the formation of burl; and it may even be that mechanical strain due to incomplete support by the roots below may be followed by woody enlargement. In all of these cases, however obscure the primary cause, we have reaction to injury experienced by the living plant.

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[80] Peirce, G. J., The Nature of the Association of Fungus and Alga in Lichens. *Proc. Cal. Acad. Sci.*, 1, 1899.

[81] Stevens, F. L., *The Fungi which cause Plant Disease.* New York, 1921.

"Witches' brooms" are the result of the reaction of the branches of trees to fungus or mistletoe infections. Latent buds develop, more lateral buds form, and a bush or brush is formed by their growth, close together, into leafy branches.

The procession of the seasons is accompanied by certain familiar phenomena, some of which are to be regarded as the reactions of plants to injury, others of which regularly precede what would cause injury if not anticipated. Autumnal leaf fall in deciduous leaved trees and shrubs is due to chilling frost, beating rain, blowing wind; but the formation of the abscission layer through which the leaf stalk breaks, and which closes the wound on the twig before the wound is made, takes place in advance of these unfavorable influences. Similarly abscission layers form at the bases of many fruits, at their junction with the stalk or at the junction of stalk and stem. Thus the plant prepares to drop its fruit without exposing itself to infection, forming an abscission layer which cuts off the fruit when ripe. The formation of such abscission layers we naturally suspect to be a reaction of stimulus. I have seen them form very quickly indeed, when gas poisoning was followed within twenty-four hours by leaf and flower fall:[82] but while these are manifest reactions to injury, the formation of abscission layers as part of the process of foliation and defoliation, and of ripening and dropping fruit, is by no means so evidently a reaction to injury, nor is it at present anything more than probable that it is a reaction to external influence of any sort. It may be an evidence of inherited habit, advantageous and perpetuated.

Leaf fall of the so-called evergreens is similarly preceded by the formation of a brittle corky layer through which the breaking off of the leaf or needle occurs; but ordinarily this abscission layer forms some time before it is needed to facilitate the fall and to prevent the exposure to infection which the usual tear or break would offer. Leaves and needles are carried by broad-leaved and needle-leaved evergreen trees and shrubs for very various lengths of time. The California live oak (*Quercus agrifolia*) drops its old leaves all together when the new crop appears in the spring. The leaves are annual in origin and duration, as in other species of *Quercus*, though they are carried through the winter instead of dropping in the fall. In orange, lemon, and grape-fruit the leaves are carried for two or more years, but all may fall after sharp frost or continued milder frost (see page 182). In pines the length of life of individual needles seems to vary according to the age of the tree, the position of the branch both as to sun and as to weight, the altitude of the situation above sea,[83] and probably other factors also. The pines carry their leaves briefly in polluted air, for much longer in clean air. For example two-year-old needles were the oldest on yellow pines (*Pinus ponderosa*) which I observed within the range of the sulphurous smoke from the smelter at Anaconda, Montana; while at Missoula, in a quite distant part of the same state, six years was the span of life.

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[82] See Crocker, W., and Knight, L. I., Effect of Illuminating Gas and Ethylene upon Flowering Carnations. *Bot. Gazette,* 46, 1908. Goodspeed, T. H., and Kendall, J. N., On the partial sterility of Nicotiana hybrids made with N. sylvestris as a parent. An account of floral abscission in the F1 species hybrids. University of California Publications in Botany, 5, 1916. See E. Lee, The Morphology of Leaf-fall. *Annals of Botany,* 25, 1911, for a description of the structure.

These and similar observations suggest that external influences, of which we are not now more aware than to guess at them, offer the irritations or stimuli to which organs and organisms react or succumb. In addition, however, to these cases of autumnal leaf-fall, of the dropping of fruit when it is ripe, of the formation of abscission layers in response to poisoning or wounding, we are familiar with the fall of whole flowers which have failed to set seed and of stamens and petals when their work has been done. Furthermore, the increase in diameter of the stems and branches of perennial dicotyledons involves the bursting of the bark unless it can continue to grow with the expanding part. The dehiscence of certain fruits and of anthers too, as suggested by Jost,[84] may be provided for mainly by the formation of abscission layers.

From the foregoing it is evident that, in the formation of abscission and similar layers, we have a phenomenon which has so far received less study than its scientific and economic importance would justify, and which should be considered, not as an isolated phenomenon appearing only in autumn leaves and ripening fruits, but in various forms in other parts and in other phases of life. According to Sampson,[84a] "the abscission of leaves in *Coleus Blumei* is a result of the conversion of cellulose into pectose, which is further transformed to pectin and pectic acid, leading to the formation of an excess amount of pectic acid over that of the available calcium sufficient to maintain the solidity of the middle lamella of the cell walls of the abscission layer. These processes are possibly initiated and probably accelerated by the presence of oxidases and ferric ions, both of which accumulate in the abscission layer."

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[83] Küster, E., *Botanische Betrachtungen über Alter und Tod.* Berlin, 1920.

[84] Jost, L., and Benecke, W., *loc. cit.*, 2, p. 249–50.

Many cases of injury are followed by substitutions rather than restorations of the injured parts. That these are reactions to the stimulus of injury is evident on careful examination of the successive changes taking place. We may recognize several types of reaction of this general sort; namely, first, the development of buds which would otherwise remain latent; second, the assumption by branches of the position of main stems or main roots; and, third, the development of flowering and fruiting branches instead of leafy ones. These must be considered separately.

Fire in the primeval redwood forest near the middle and northern coast of California seldom causes the death of the trees, but it destroys the leaves, twigs, many of the smaller branches, and may even kill all the branches of the main trunk. There remain after severe fire, then, the blackened columns which were the trunks of redwood trees. Presently a veil of green is put out over each trunk, the buds long latent reviving their activity, growing out through the thick bark into the air, these twigs bearing leaves and growing on into branches normally leafy. So the "fire columns" gradually grow into trees once more, though they may have gone through fire which would have killed other trees with thinner or more resinous bark.

[84a] Sampson, H. C. Chemical changes accompanying abscission in Coleus Blumei, Bot. Gazette, 66, 1918.

Fire which defoliates *Eucalyptus globulus,* the "blue gum" of the antipodes, and perhaps destroys the youngest branches, will be followed by a similar growth veiling the trunk and growing out ultimately into normal branches and foliage. The leaves first put out, however, are not the usual pendent bifacial slender ones, green in color, but strikingly blue-green, glaucous, broad, and horizontal leaves, precisely the form developed by the seedlings and carried by them until the very rapidly growing saplings begin to take on adult characters. Similarly if blue gum is cut down to a height of ten or a dozen feet from the ground, as is commonly done, furnishing an admirable fuel, stump-sprouting will occur, the latent buds developing, as after fire, and the branches bearing the juvenile form of foliage. The juvenile and the adult foliage of this species are so strikingly unlike in appearance and structure that speculation as to the cause has not been lacking[85]; but experimental investigation awaits the curious. Similar speculation about the corresponding but far less striking juvenile foliage of redwood[86] and of the pines deserves critical attention, and the study of the behavior of these plants under and after adversity in the conditions of to-day may suggest new thoughts as to the conditions of the past in which they were apparently more important than now.

On the other hand, if anything happens to the tip of a shoot, or of the main shaft of stem or root, so that growth is checked or prevented, the formation, development, growth, and competition of branches becomes a familiar and striking phenomenon. The production of hedges, in horticultural practice, depends upon the more abundant growth of laterals following amputation of the main shoot or shoots. The pinching back of the florist, professional or amateur, is followed by similar branching and the production of stockier plants. The loss by lightning, wind, or topping, of the tip of the main stem of a tree of excurrent habit is followed by competition among the side branches for the succession as leader in the growth upward. In deliquescent stems such competition occurs without noticeable external influence; yet in these, as in the others, the loss of the leadership by the main shoot, whether caused by accident or occurring normally, is reacted to by the side-branches, the rate and direction of their growth changing in response to the change in circumstances.

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[85] Bower, F. O., *The Botany of the Living Plant,* p. 177. London, 1919.

[86] Jeffrey, E. C., *The Anatomy of Woody Plants.* Chicago, 1917.

If the growth of the main shoot or the main root is experimentally or accidentally checked, for example by a root tip growing against a stone or by a stem being temporarily injured by frost, the laterals will promptly attempt, by increased growth and changed direction, to take the place of the incapacitated leader. This reaction to injury, tending to result in the substitution of a branch for the main stem or root, is followed by competition for place, struggle for existence, in a form not evident before in these individuals. The injury harms not only one part or organ; it also destroys the balance, the coördination, previously prevailing among several or many organs. Competition, struggle, occurs at once and continues until a new balance is attained.

Presumably closely related to these reactions, perhaps indicating the basis for them, is the behavior of roots when subjected to bending. According to the experiments of Noll[87] the roots of lupine seedlings, forcibly bent in bow or spiral form, branch only on the convex portions. Various explanations of this behavior have been offered[88] but the question as to its cause is still unanswered. Goebel's idea that differences in the amounts of foods reaching the convex and concave parts, and Noll's idea that the different tensions in extended and compressed tissues influence branching, are not composed by Klatt[88] who finds the branching of longitudinally split roots is quite uniform along the course of the bends.

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[87] Noll, F., *Landw. Jahrbücher,* 29, 1900: Gertz, *Lunds Univ. Arsskv.* 10, 1914; Lundegårdh, *Archiv f. Entwickelungmechanik,* 35, 509, 1913.

Decapitation of the main root is followed, as we have seen, by the development of branches; forcible bending without any injury to the tip is also followed by branching; but injury to the tip may be followed, not by branching but by restoration, restitution, or rejuvenation of the injured organ. We see, then, that disturbance of the balance whether of tissue tensions, of food supplies, or of exposure to the air, constitute injury and will be followed by pronounced activity in adjacent parts capable of growth; but the nature of the reaction, whether substitution or restoration, will vary with the injury, but in any case will be new growth.

Corresponding injury to the tips or upper parts of stems is often followed by the formation of so-called suckers or stump-sprouts. Whereas most coniferous trees are incapable of vegetative reproduction, the redwood and California nutmeg (*Tumion*) distinguish themselves by such vigorous stump-sprouting that the redwood forest may be restored after cutting or the nutmeg tree replaced in time.[89] Obviously, these stump-sprouts or suckers come from hitherto latent buds, called into activity by the injury to the top of the tree. Their development is of great economic importance. If an area of redwood forest lumbered over is cleared up in such manner that the stumps and underground parts are not killed by excessive heat,[90] vigorous new growth will be sent out from the old parts. This new growth, nourished on the food stored in the old parts and only made available when needed,[91] will make merchantable timber in the course of thirty to fifty years. There is, therefore, no need of the redwood ever dying out if it is so handled in lumbering that its surviving parts can react, instead of succumbing, to injury.

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[88] Goebel, K., *Einleitung in die Experimental Morphologie.* Leipzig, 1908. Klatt, A., Ueber die Entstehung von Seitenwurzeln an gekrümmten Wurzeln. *Ber. d. d. bot. Ges.* 27, 1909.

[89] Jepson, W. L., *Silva of California.* Univ. California, 1910.

Horticultural practice has long included, under the names of cutting back, thinning, pinching out or pinching back, and pruning of stems, to mention only these, various mechanical processes designed to increase the number and quality of the flowers and fruit produced. In the practice of pruning, for other purpose than merely modifying the form of a plant by mechanical means alone, the desired result may be the resultant or composite of reactions to several or many stimuli, rather than the reaction to any single stimulus. Reflection shows that we can distinguish at least these consequences of the mechanical process of cutting off employed in pruning: 1st, the wounding of various organs and their component tissues; 2nd, the reduction of the food-manufacturing and water-evaporating tissues and organs; 3rd, by the reduction of the food-consuming tissues the release of a larger amount of stored foods and water for use by the surviving parts; 4th, the opening or exposing of the whole plant above ground to more light, more air, and more water loss by evaporation; 5th, the changes in the amounts and kinds or directions of mechanical strains to which all parts, underground as well as above, are subject. (See pages 239–247.) Obviously, only the irritation of the wounds themselves is confined to the seat of injury, while other effects may be extended to more distant, and some to all, parts of the plant.

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[90] Peirce, G. J., Studies on the Coast Redwood, *Cal. Acad. Sci.*, 3d Ser. Bot. 2, 1901.

[91] Peirce, *loc. cit.* Miehe, H., Ueber die Lebensdauer der Diastase. *Ber. d. d. bot. Ges.*, 41, 1923.

Pruning as practiced in this country on young stock checks or removes the purely vegetative branches, exposing the fruit buds. Subsequent to the amputation of the vegetative branches the flower buds below the wounds develop. Flowers and fruit "spurs" are or may be already present on the young trees; but they may be formed in larger proportion in succeeding years as a consequence of expert pruning; and old trees may be "rejuvenated," that is, may be stimulated to form an increased number of fruiting branches, by thorough pruning or cutting back. In addition to the mechanical injury, the direct effect of which is mainly local, the changes in water consumption and loss, in oxygen and carbon dioxide ventilation, and in illumination, by thinning and opening the opaque dome of foliage, are so considerable as to arouse suspicion that they are all involved. Aeration and ventilation are evidently increased, with corresponding change in water loss. The possible effects of increased illumination upon the production of flowers, and hence of fruit, will be considered later. Enough has been said already, however, to indicate that this familiar and economically very valuable procedure involves much more in the way of reaction to stimulus on the part of the plant, than at first glance appears to be the case.[92] It would be wise for the plant physiologist to follow the pomologist in a restudy of pruning, for theoretical and practical results of importance promise to repay such study.

In addition to the evident formative influence of injuries of various sorts, the direction of growth may also be affected. Darwin [93] found that the direction of growth of the roots which he was studying could be influenced by mechanical, chemical, and physical agents which he applied to the tips. Spalding [94] extended and confirmed Darwin's results, but there has seemed little reason or encouragement to study this phenomenon in such slowly moving organisms as plants. The impressive name, traumatotropism, has marked the stopping point of investigation of the subject, for though more has been written upon it,[95] little new has been learned. Traumatotaxis is also of such minor importance among plants as to have received slight attention, except as one may call the movements of cell parts in response to injury to the cell traumatotactic.[96] Thus we have studies of the movements of nuclei, or of chromatophores, or of other bodies, following the cutting of the cell wall and very probably the destruction of the whole balanced and self-operating system of the cell. This constitutes a new and valuable form of study, known as micro-dissection; [97] but while some of the reactions of the parts may make up the response of the whole organism, they do not constitute subjects of study similar to those hitherto considered, and they should be clearly distinguished.

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[92] For discussion of the subject from the practical side see *The Pruning Manual*, by L. H. Bailey, Macmillan, 1916 or later; from the theoretical, Molisch's *Pflanzenphysiologie als Theorie der Gärtnerei*, 4th ed., Jena, 1921; and Hooker, H. D., Jr., Changes Produced in Apple Trees by Various Types of Pruning. Univ. Missouri, Coll. of Agric., Agric. Exp. Station, *Research Bull.* 72, 1924.

[93] Darwin, C. and F., *The Power of Movement in Plants.* New York, 1881.

[94] Spalding, V. M., The Traumatropic Curvature of Roots. *Annals of Botany,* 8, 1894.

[95] See Stark, P., Studien über traumatotrope und haptotrope Reizleitungsvorgänge. *Jahrb. f. w. Bot.* 60, 1921.

[96] Němec, B., *Reitzleitung und reizleitende Strukturen,* Jena, 1901.

[97] Taylor, C. V., Demonstration of the Neuromotor Apparatus in Euplotes by the Method of Micro-dissection. Univ. of California *Publications in Zoölogy,* 19, 1920. Also *Science,* 51, 1920; *Journ. Exp. Zoöl.,* 37, 1923, etc.

IX

IRRITABILITY

The Radiant and Chemical Influences

In certain respects of fundamental importance light differs in itself from the forces or phenomena which we have hitherto examined. In consequence, its effects are correspondingly different. Light is not constant, uniform, irreversible, indivisible, inescapable, but periodic though unchanging. These statements need amplification and precision, for we do not clearly and fully apprehend the solar radiation to which we are daily exposed.

Excepting from discussion, for the time, those solar radiations which are termed electrical, and confining ourselves to those forms of energy of solar origin which may be seen by the eye, revealed by the thermometer, or recognized by photography, we realize that there is coming to the earth constantly an enormous amount of energy. This, because of the movements of the earth, is not constantly received by any one part; nor are equal amounts received by equal parts because of differences in position; nor, because of atmospheric differences, is the total radiation, as to quality or as to quantity, always received by a given area of soil. There result, then, the diurnal alternation of day and night, the seasonal alternation of summer and winter, and the larger and larger cycles, if any, to and including the glacial and non-glacial epochs which the earth has experienced. The periodicity of light is in marked contrast to the constancy and uniformity of gravity. Furthermore, northern, southern, and equatorial positions on the earth entail general differences in exposure to light. These are much more considerable than those due to differences in exposure consequent upon topography, forest cover, or other local differences. Finally the air is different in its components and qualities over different parts of the earth's surface.

Owing to differences in topography, the different parts of the earth's surface are overlain with air of different depths. The layer of air, for example, over the Salton Sea in Southern California is 250 feet thicker than that which overlies the Gulf of California or the Pacific Ocean; and it is 20,000 feet thicker than the layer of air which covers the summit of Mt. Everest. Since air is not perfectly transparent, as shown by the blueness of the sky and by the limits of vision, it is obvious that, other things being equal, less light will reach sea level than will fall upon a mountain peak in the same latitude. Among the things not equal, however, are the components of the air. While the proportions of nitrogen, oxygen, and carbon dioxide are the same anywhere, the proportions of other things, especially of water vapor, vary greatly both from time to time and from place to place. In consequence, the quantities and qualities of light falling upon equal areas of Nevada desert and of Connecticut valley farm land would be unequal, even if they were at the same altitude and on the same parallel of latitude.

Unlike gravity, light is made up of unlike components. A beam of ordinary daylight is thought to consist of rays of different wave lengths which correspondingly affect the human eye and the other sensitive structures which they reach. The rays may be separated by prismatic means (prisms, gratings, films) into more or less complete and perfect spectra, or they may be more or less selectively absorbed by so-called colored objects. The effects of light are therefore the effects of its component rays, warming, lighting, and chemically changing the materials upon which they fall and into which they penetrate. If one attempt to measure gravity, the problem is comparatively simple; if one attempt to measure light, the problem is complicated because there is no single instrument which will measure heat, light, and chemical rays with equal completeness and accuracy. Hence we have no photometers equal in accuracy to thermometers, speedometers, electrometers, etc. The various attempts to indicate, as quantities of energy or in any other way, the total amount of light and the fractions of the total contributed by the different components, are only partially successful. The effectiveness of different kinds of electric lamps formerly indicated in candle power is now stated either in watts or in volts; but in these terms there is little indication of the amount or kind of work that can be done by the light. The small six to eight volt bulb used as an automobile headlight is very effective, but it would be of little value in lighting a room, in printing photographs, or in warming an oven.

In studying the influence of light, in addition to its duration, intensity, and composition, its direction must also be taken into account; for although light comes primarily from the sun or from the sky, it is so impeded and so reflected in its course that it may finally reach an object from the direction opposite to that from which it started. If it act as a stimulus and provoke a reaction, the place, direction, and other features of the reaction may be determined by the direction of illumination (see pages 315–317).

The effects of light may be classed as *formative* and *directive*. Beginning with the former, which are less familiar, perhaps because they have been less discussed though they are no less striking, we may make those distinctions in the influence of light already suggested, namely as to the *quantity* of light, its *quality*, and its *direction*. By quantity of light may be implied intensity or duration or energy total. An intense illumination of brief duration may or may not equal in its effects less intense light playing longer upon a given object. The question at once suggests itself as to whether the total amount of energy is not the determining factor, quality of light and other things being equal. The recent investigations of Blaauw [1] and of others following him [2] confirm this, but as these authors show, the quantities may be remarkably small. This will be illustrated in the following.

The spores and seeds of certain plants have long been said not to germinate in darkness (for example the spores of some ferns and *Viscum* seeds) while certain others seem to be delayed or prevented in germination by light.[3] Experiment shows, however, that, by modifying the conditions, germination may nevertheless take place. As these results are of practical importance to growers — seedsmen, nurserymen, florists, farmers, etc. — we may refer to Molisch [4] for his summary. The subject is now undergoing renewed study, with the application to it of the newer methods of experimentation, so that we may expect valuable results presently. In this as in all other study of light, the effects of the different rays must be distinguished.

The germination of spores and seeds, and the opening of buds, involves so many processes, physiological and chemical, and so many external factors, that general statements even as to the effect of single factors are scarcely possible. For example, the rays at the red end of the spectrum apparently expedite, while both blue and violet rays delay, or even prevent, germination. Furthermore, the opening of buds seems similarly to be influenced by light and by its component rays.

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[1] Blaauw, A. H., Licht und Wachstum. III. Wageningen, 1918. Recherches et theories sur le sensibilité physiologique. *Archiv du Musée Teyler*, Ser. 3, vol. 3, 1915.

[2] Buder, J., Neue phototropische Untersuchungen. *Ber. d. d. bot. Ges.*, 1918. Koningsberger, V. J., Lichtintensität und Lichtempfindlichkeit. *Recueil des travaux bot. néerl.*, 20, 1923.

[3] Kurzel, W., *Frost und Licht als beeinflüssende Kräfte bei der Samenkeimung.* Stuttgart, 1913.

[4] Molisch, H., *Pflanzenphysiologie als Theorie der Gärtnerei,* 4te. Aufl., 1921.

The influence of light upon the quantity of growth is so commonly recognized that certain striking results are often attributed to light which more properly may be charged to increased water loss. Thus the shortening flower stalks of the various weeds as the dry season comes on in this part of California may be partly due to increased light as the days lengthen, but it is also undoubtedly due in part to the increasing transpiration with decreasing soil moisture. Tulips planted in the gardens of this region do not generally develop as long flower stalks as elsewhere. It is common practice, therefore, to plant the long-stalked Darwin tulips in preference to the Cottage and other short-stalked varieties. Comparison of the temperatures and humidities prevailing when the tulips are blooming here, and in New England for example, will show that higher temperatures and lower humidities prevail here than there. At the same time, however, the amount of light is greater here than there. We have, therefore, the combination of many factors determining the length of the flower stalks of individuals of common heredity. The combination of light, temperature, humidity, and soil in Holland has made it peculiarly suitable for bulb-production. Such conditions are not general elsewhere.

It is common observation that the stems of plants receiving insufficient light are long, slender, "drawn." This shows itself under cultivation in greenhouses and gardens, but it is a perfectly natural phenomenon out-of-doors. Forest, brush (chaparral), climbers, and erect plants show this on the great scale, and the making of a hedge shows it in cultivation.

While it true that in forest, chaparral and grassland, transpiration, temperature, and humidity are characteristically different and influential, it is also true that the light is also; and in the straight tall boles of a close stand of pine and the slender stalks of corn in the row we see the formative effect of dim light as compared with the full light which falls on the single tree or the solitary corn stalk. In unmixed forest, and in brush or chaparral composed of plants generally alike, we see the formative influence of light in the height also; for the top of the forest, and of the chaparral, is fairly even, resembling a coarse lawn in the uniform height of its components. This effect is frequently shown also by those plants which invade more solid stands. Geraniums which reach the usual height in the garden may run to twice this height when growing in a privet hedge: or bur clover (*Medicago denticulata*), which is ordinarily prostrate, forming low pads close to the ground, may be six feet tall in a hedge; and the California poppy (*Escholtzia californica*), which may be a foot or so tall in the fields, may be six or more feet tall in chaparral. Poison oak (*Rhus diversiloba*) is here generally erect and self-supporting in the open; but I have seen it climb to seventy or more feet on the somewhat shaded trunk of a redwood. The castor bean grows vigorously erect and stocky in the well-lighted garden, but in shade takes on a slender and prostrate or leaning habit.

At the same time that the quantity of light seems to determine the amount of growth in stems, as above indicated, a great amount or great intensity of light tending to check, a lesser amount tending to promote growth in length in stems, it should be remarked that light may promote the growth in thickness of stems, and that it certainly promotes the growth of leaves in size. The leaves of " drawn " stems are smaller than those on thicker, sturdier stock. For many years the loose generalization has been accepted that light checks growth and darkness favors it. Based on faulty methods of experimentation, and expressed in undiscriminating terms, this classic generalization of the great Sachs must be qualified or abandoned altogether. Jost[5] suggests that one must distinguish between organs of unlimited growth (like stems and roots) and organs of limited growth (like leaves and sporangiophores). While this may be advantageous, the distinction is not without exceptions,[6] for the prothalli of ferns have been found to grow larger in more generous illuminations; and under conditions favorable for growth but not for fertilization, they have been known to grow indefinitely in size and duration.[7]

It is stated that the growth of roots and of root-hairs or rhizoids is favored by less than the maximum illumination, that their formation and growth take place on the side of the organ which is away from the light. This is generally true. The prothalli of ferns develop not only rhizoids but also archegonia and antheridia on the side away from the light, when there is any difference between the two sides. Under natural conditions more light comes from the sky than can be reflected from the soil upon the face of the prothallus toward it; but if the spores are sown on suitable substrata upon turn-tables,[8] so that the growing prothalli receive approximately equal illumination on their two faces during the hours of daylight, rhizoids, archegonia, and antheridia form equally on the two sides. With the improvements in artificial illumination which furnish light more nearly approaching the requirements of green plants, the cultivation of fern prothalli under constant and equal illumination from the spore stage promises information on the influence of light upon the formation of rhizoids and reproductive organs not to be expected before. Thus the researches of Klebs [9] are a very valuable resumption and extension, under improved conditions, of investigations hampered by difficulties now reduced.

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[5] Benecke-Jost, *Pflanzenphysiologie*. Bd. 2, p. 45, 1923.

[6] Peirce, G. J., *The Formative Influence of Light*. Dudley Memorial Volume, Stanford University, 1913.

[7] Campbell, D. H., *Resistance of Drought by Liverworts*. Torreya, 4, 1904.

[8] Peirce, G. J., *The Formative Influence of Light*. Dudley Memorial Volume, Stanford University, 1913.

The long known differences in size, texture, and structure of the " sun " and " shade " leaves of the same plant, first reported perhaps for the beech [10] but well known in many other cases, has been attributed, as the names imply, to differences in exposure to light. But as has been pointed out before (pages 300 ff.), the differences in light are necessarily accompanied by differences in temperature and transpiration, and the character of the leaves is necessarily influenced, if not determined, by all three. The formation of " water sprouts " by citrus trees is common. These bear, under the shade of the dome of foliage, leaves which are larger and more tender than those borne by the other branches of orange, lemon, and grapefruit trees. The " water sprouts " and their foliage are, however, considered to be of less value to the plant than the outer shoots with their smaller, tougher, and better lighted leaves. If one examine the outer leaves of well-sunned citrus trees one will find two or even three layers of palisade cells, with corresponding sugar and starch formation. In less abundantly lighted situations, however, the formation of palisade cells and layers is less. This is true of individual trees less well lighted in the same grove and generally true of the trees in regions of less brilliant sunshine, less heat, and more moisture (compare for example the foliage of orange trees in this region and in southern California).

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[9] Klebs, G., *Zur Entwickelungsphysiologie der Farnprothallien.* Sitzungsber. d. Heidelberger Akad., 1916, 1917.

[10] Stahl, F., Ueber den Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter. *Jenaische Zeitschr. f. Naturwiss.*, 16, 1883.

The flattened form of the "joints" of certain cacti, ascribed by Goebel[11] to the influence of light because they form only in the light, is another example of a too simple explanation being offered for a complex phenomenon. If one enclose a young, growing "joint" in a light-proof cover, one necessarily cuts off the access of heat rays, thereby changing the internal as well as external temperatures of the joints,[12] as well as the transpiration. Furthermore, the difference in the quantity of immediately available foods in such unnaturally darkened and in the normally lighted green joint is not without its effect. Goebel was led by his interpretation of the results of his experiments to consider the radial structure of the undeveloped darkened joints as "reversions" to the original structure of these cacti. While this conception is plausible it may well be questioned (see page 290).

Such vines as the Boston Ivy (*Ampelopsis Veitchii*) and English Ivy (*Hedera helix*) attach themselves to their supports by means of tendrils and roots respectively. Experience has shown that, in certain climates, attachment is not effected if the support be so white and smooth that much light is reflected from it. In other words, the attachment takes place on the darker side. Contact with the support is established by the formation of roots on the dark side of the English Ivy and by the turning of the tendrils away from the light (negative phototropism, to be discussed on pages 317 ff.) in the case of the Boston Ivy; but the reaction to contact (see page 265) follows the reaction to light.

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[11] Goebel, K., Ueber die Einwirkung des Lichtes auf die Gestaltung der Kakteen und anderer Pflanzen. *Flora,* 80, 96, 1895. *Organographie der Pflanzen.* 2te Aufl. Bd. 1, p. 485, 1913.

[12] MacDougal, D. T., A New High Temperature Record for Growth. *Science,* 53, 1921.

In this same connection one may speak of the phenomenon sometimes called etiolation. Horticultural practice resulting in the production of "blanched" celery and asparagus represents the extreme, in which chlorophyll formation is prevented as well as the development of those tissues directly and indirectly dependent upon the formative stimulus of light. Between this and the various degrees of "drawing" (see page 300) there are all stages to be found in nature, or they may be produced in cultivation. An amount of light ample for chlorophyll formation (see page 77) may be such that in air of considerable humidity and at moderate temperatures stem growth may be considerable. In a winter characterized by mildness and rain the garden nasturtiums (*Tropæolum majus*) grew here rank and green, flowerless, with large succulent leaves and long soft stems. Unless one choose to limit the meaning of the word etiolation to the suppression of chlorophyll formation, one must consider "drawing" and the related phenomena as being also included. Given the corresponding temperature and humidity, the quantity of light will determine the degree of etiolation, the amount of "drawing" of stems, the size and other characters of the leaves, of land plants.

There has been much discussion in recent years of the relation of light to the production of bloom. This is based on the experimental work of Klebs and others on the algæ,[13] and Vöchting and others on flowering plants,[14] as well as on the practical experience of commercial florists and other horticulturists (fruit growers) and the unnumbered observations of botanists and others in all parts of the world. We may begin our consideration of the influence of the *quantity of*

[13] See Oltmanns, F., *Morphologie und Biologie der Algen*. 2te Aufl. Jena, 1922 +.

[14] Vöchting, H., Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen. *Jahrb. f. w. Bot.*, 25, 1893.

light upon the *kind of growth* by referring to the observation in the previous paragraph that in a mild, rainy, and therefore relatively dark, winter here the garden nasturtiums vegetated luxuriantly but were flowerless. The opposite of this condition prevails wherever there is a great amount of light with relatively less moisture in both air and soil; for under these conditions the garden nasturtium is comparatively short, with smaller leaves, and an abundance of blooms. Under these conditions there is no "drawing," there is compacting if anything, of the stem; but is the abundant light the stimulus to bloom? This question can be answered when observation under natural conditions is informed and confirmed by experiment.

It has long been remarked that at high altitudes, the herbaceous plants are stocky and yield in proportion to their size an abundance of bloom. Pistillate and staminate cones of the conifers growing high up in the mountains are noticeably abundant (compare the production of pistillate cones of *Tsuga* at the top and at the bottom of its range in the Sierra Nevada Mountains). In the Alps, the White Mountains of New England, and the Sierra Nevada Mountains of California I have observed this to be the case. If one compare the vegetation of valley and peak, differences corresponding, not to the altitude as such, but to the results of the altitude in temperature, water relations, and especially light, will attract attention. Granting that, if plants are to produce equal amounts of bloom, they must bloom more abundantly during a brief season than if conditions permit an extended period, yet examination will show that the proportion of bloom is actually as well as relatively greater on the more abundantly lighted mountain peak than in the valley. The difference in the amounts of light in the two situations may be indicated by the time of one hour and a half between sunrise and sunset in the short winter days at the head of the Lauterbrunnenthal in the Swiss Alps and the hours between sunrise and sunset at the same season elsewhere in that latitude.

Travelers have commented upon the prodigal bloom of Arctic regions as contrasted with the relative absence of bloom in the humid tropics. A part of this difference undoubtedly lies in the crowding of all the activities of nearly all the organisms living in the Arctic into the few months of summer. There is similar crowding in other parts of the world where winter squeezes the summer by prolonging the spring and shortening the fall. One may see in places in the Sierra Nevada, the flowers of spring, summer, and autumn simultaneously. But the abundance of bloom in the Pacific states and in the arid and semi-arid states of the Inter-Mountain Region and the southwest, so vividly described by naturalists[15] and travelers, cannot be accounted for on the basis of a short season, the crowding of bloom into a brief period limited by winter frost and summer drought. On the contrary, bloom might regularly take place earlier if, as is the case in seasons of scanty rainfall, there were in winter the amount of sunshine which ordinarily comes later. In fact, spring and its bloom come early or late in this part of California, not according to the temperature or the length of day, but according to the time when the rains cease and there is abundant sunshine (light).

This conclusion as to the influence of light on the production of bloom is confirmed by the seed industry, by the growing bulb industry, and by the observations of botanists particularly interested in the flowerless plants. Flower, vegetable, alfalfa, and certain other seeds are increasingly the products of the " far west " so far as this country is concerned. Wheat and other grains bred to meet the special conditions of Kansas, the Dakotas, and Canada, have so far been produced where they were needed: but onion, lettuce, and other vegetable seed are increasingly produced for the rest of the country in California, while alfalfa seed can apparently be best produced on the shores of Great Salt Lake, provided the parasites (weevils, dodder, etc.) can be duly controlled. Sweet pea and other flower seed farms attest the recognized commercial value of ample illumination. The very specialized bulb industry finds increasing advantage in a region where the quantity of light available is so great owing to the climatic conditions.

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[15] Muir, John, *The Mountains of California.* New York, 1901, 1913, 1921.

It is a matter of record, confirmed by repeated observation,[16] that the mosses, liverworts, and ferns of this region fruit with a degree of regularity and an abundance quite unknown in other parts of this country. It need not be questioned that this result is in part due to the mildness of winter, which not only is not destructively cold, but also permits photosynthetic and other activities on most days throughout the season. In addition to this, and to all the other factors favoring fruiting, it should be recognized that more light reaches the surface of the earth in dry climates than in damp. Moisture may exist in the air as invisible vapor or as cloud, in either case absorbing light. The absorption, both as to quality and as to quantity, will vary with the condition of the moisture, clouds evidently absorbing more light than water vapor does. The absorption of a saturated though cloudless atmosphere is nevertheless very considerable. Furthermore, heat, light, and chemical rays not being equally absorbed, the quality as well as the quantity of light reaching the soil will vary. While it is at present impossible, owing to the difficulties already described (page 298), to express the differences in definite terms, one may nevertheless state that more light falls here per annum than on corresponding areas east of the Rocky Mountains. The traveler eastward bound may notice that, as he leaves the dry far west and approaches the Missouri River, the air is less translucent, the sky less blue, the landscape darker.[17] As one continues eastward the effect becomes more and more pronounced. This impression is confirmed by photography; a time sufficient for exposure in this region will give under-exposed negatives in the Mississippi Valley and on the Atlantic slope, and exposures timed as in the east yield over-exposed negatives in this region.

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[16] Campbell, D. H., *Structure and Development of the Mosses and Ferns*, 3d ed. New York, 1918.

We are, then, justified in concluding that light may be the factor determining the extent to which plants will bloom and fruit in a given region.

These observations and the conclusion thus drawn from them are confirmed by experiment. In the experiments of Klebs[18] and others it is shown that light is one of the factors determining whether an alga shall reproduce itself and the particular mode by which it shall be accomplished. It appears that while reproduction may be accomplished without exposure to more light than sufficient for photosynthesis, the more vegetative modes will be the ones developed, the formation of the sexual organs taking place only after sufficient stimulation by light. Similar results are reported by Vöchting[19] who experimented with flowering plants. He found, for example, that *Mimulus Tilingi* would vegetate indefinitely in the north greenhouse attached to his laboratory in Tübingen, in south Germany, but would begin promptly to form flowers when transferred to the better lighted house at the opposite end of the building.

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[17] Neither coal soot nor other products of man's activities are meant, for I am suggesting a comparison of clean country air in these different regions.

[18] Klebs, G., *Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen.* Jena, 1896.

[19] Vöchting, H., Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen. *Jahrb. f. w. Bot.,* 25, 1893.

In the arid west irrigation projects have converted extensive areas previously desert into most productive farming, trucking, or fruit-growing areas. In some of these the soil is notably fertile, having been deposited as silt by repeated overflows of streams; but the major part of the areas reclaimed from the desert by irrigation are notably deficient in one or more of the constituents of fertile soil.[20] Nevertheless, it is literally true that, by the addition of water, the desert has been "made to blossom as the rose." Its productivity cannot be maintained without fertilizing as well as irrigating; but given the necessary raw materials for food production, these areas reclaimed by irrigation are tremendously productive of those crops dependent upon flowers, that is, upon the organs of sexual reproduction in plants. The so-called root crops do not profit as greatly from the brilliant illumination of these irrigated areas. Potatoes, requiring better soil, do not need intense illumination for the formation of tubers. Grain, melons, the small fruits (berries), and the larger fruits both deciduous and citrus, bloom profusely. Prolific bloom is not invariably followed anywhere with a correspondingly heavy set of fruit, and yet the productiveness of these regions is generally recognized. The irrigated areas of the arid and semi-arid far west, of Egypt and of India, then, confirm by an experiment on the grand scale out-of-doors, the conclusions drawn from the laboratory experiments of Klebs, Vöchting, and others, from the observations of botanists and others in nature and in cultivated areas, that light is especially the stimulus to the production of the sexual organs of both flowerless and flowering plants.

Ireland, Maine, and certain other regions noted for clouds and dampness rather than for brilliant sunshine, are the principal producers of potatoes. Grain, except sweet corn for table use, is largely a western product. Vegetables must be produced near the market if they are not to bear an excessive price. The same economic consideration applies to fruit. In spite of this, the fruit of Europe and of America, and much of the vegetable supply of both continents, are the product of the better lighted regions. It is not alone the mildness of the shores of the Mediterranean which has made them the garden of Europe; it is their light (*cf.* p. 313).

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[20] See Hilgarde, E. W., *Soils*. New York, 1906.

A distinction was suggested above between light sufficient for photosynthesis and light as a stimulus to fruiting. It is claimed that fruiting is regulated by the food supply, which is evidently dependent upon photosynthesis, and that the distinction suggested is not valid because more light means merely more photosynthesis and more food.[21] Such a claim is not substantiated by observations in the field and in nature; for one has often seen plants of all sizes, from grain to trees, putting forth bloom quite without relation to the amounts of food in the plants. Thus, the stunted plants of a grain field in a season of insufficient rainfall, fruit trees about to die from mechanical injury or from certain forms of disease, and trees not killed but dying after forest fire, may be seen to put forth bloom quite out of proportion to the food which they have recently made or even which they have accumulated and stored in the course of years.

Garner,[22] in a series of very interesting studies with Allard of what they call *photoperiodism,* shows that many plants come into bloom according to the length of the period of daylight. Working, for obvious reasons of convenience, mainly upon short-lived annual plants, they connect the habit of blooming in spring, summer, or autumn out-of-doors, or at one or another of these times under glass, with the number of hours of daylight when their experimental plants germinate from the seed and grow. By shortening the daily period of daylight by keeping the experimental plants in darkness for a part of each day, and by lengthening the daily period of illumination by means of electric lighting, they find that various features of the usual behavior of plants can be correspondingly modified. They point out that the periodicity of light, and the periodicity in the growth, blooming, setting of seed, formation of tubers, etc., coincide. In agreement with Klebs and Vöchting they ascribe to light the stimulus to bloom, but by reason of the methods employed they were not able to show that the quantity and the quality of light profoundly influence the quantity of bloom. Thus, their experiments were mainly if not entirely conducted in one spot, the climatic conditions of which are essentially similar year after year; and to increase the period of illumination they employed forty watt Mazda bulbs from sunset till midnight each day. " The average intensity of the electric illumination maintained in the vicinity of the plants in the greenhouse was approximately three to five foot candles." It goes almost without saying, however, that while this light may seem brilliant to the eye, because of its evident and dazzling points of origin, the total is far less than that of ordinarily diffused sunlight.[23] Therefore their lengthening of the day could not greatly influence blooming although it plainly influenced the time of blooming. On the other hand, that the quantity of bloom may be greatly increased or diminished by the quantity of light has been shown above, and would be plain to Garner and Allard if they would extend their experiments westward, along the same parallel of latitude as Washington.

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[21] Kraus, E. J., and Kraybill, H. R., Vegetation and Reproduction with special reference to the Tomato. *Oregon Agric. Coll. Exp. Sta. Bull.* 149, 1918.

[22] Garner, W. W., and Allard, H. A., Further Studies in Photoperiodism. The Response of the Plant to Relative Length of Day and Night. *Journ. Agric. Research,* 23, 1923. See also Adams, J., Duration of Light and Growth. *Annals of Botany,* 38, 1924.

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[23] This is estimated to be about 10,000 foot candles in direct sunlight in summer in England, several thousand with clouded sky, three foot candles in a building artificially lighted. See anonymous article in *Nature*, 114, p. 732, 1924, The Effect of Artificial Light on the Growth of Plants.

We come now to a direct consideration of the quality of light. Of the total luminous solar radiation only those rays reach the earth's surface which are not absorbed by the components of the earth's atmosphere. In addition to that general stratification of the earth's atmosphere believed to prevail all around the globe there are local differences, transient or persistent, all of which necessarily affect both the total quantity of energy in the form of light and also the quality, as indicated by the wave lengths reaching different parts of the earth's surface. Comparison of photographs of solar spectra taken in summer at the Mt. Wilson Observatory in southern California and at observatories in the Middle West, the Eastern States, and in Europe, would show extensions beyond the usual spectrum, both below the infra-red and beyond the ultra-violet, the latter being the more marked, in the Mount Wilson photographs. Granting that the elevation of Mount Wilson above the plain entails less absorption of light than takes place at lower altitudes, that latitude also has its effects in length of day, etc., the fact remains that more light penetrates dry air than through an atmosphere of high humidity, and that this light, though falling for the number of hours per day fixed by the latitude, is brighter, more intense, richer in its range of rays of different wave-length than light falling through the moister air of other parts of the world.

The observations of Klebs[24] on the influence of light of different qualities (wave-lengths or colors) and intensities (amounts of energy), making use of more accurate means of quantitative determination, show that spore-germination, cell-division, cell-growth, the growth of the plant body — in this instance the prothallus — in length, breadth, and thickness, and the formation of the organs of sexual reproduction, are profoundly affected by the amounts and the qualities of light. While Klebs shows that the result of exposure to certain rays is not always the same, irrespective of other circumstances, he goes far toward establishing as fact that, other things being equal, the effects of these rays will always be the same. Thus he shows that, under ordinary conditions, fern spores will not germinate in darkness, but illumination with blue, violet, and ultra-violet light does not stimulate them to germinate. On the other hand cell division and cell differentiation are more influenced by light rays of the shorter wave-lengths (blue, etc.) than of the longer (red, etc.).

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[24] Klebs, G., Zur Entwickelungsphysiologie der Farnprothallien. *Sitzungsb. d. Heidelberger Akademie,* Math. Naturw. Klasse, B., 1916, 1917.

Klebs's work in this direction, stopped by death, has opened a field in which much work of great importance can be done.

As shown recently by Guttenberg[25] another factor must be taken into account in light studies, at least of massive plants, namely the size of the illuminated area. Thus Guttenberg shows that the quantity of energy received as a stimulus by a plant may be regulated by the intensity of the light, the duration of the exposure, and by the area of the exposed surface. The behavior of the plant will correspond.

As already pointed out (pages 302–303), the formation of vegetative and reproductive organs seems ordinarily to be determined by light, rhizoids and roots, archegonia and antheridia, forming on the darker side of the mosses, liverworts, ferns, etc. It has also been shown, in certain instances at least, that the form of the plants themselves is profoundly influenced by the direction from which light comes. There are two types of plant structure, the radial and the dorsi-ventral. Erect organs of land plants tend to be radial, the horizontal or oblique organs dorsi-ventral in structure. In addition to the easily conceived mechanical influences tending toward these respective results (see pages 237–247 under Gravity) experiment shows that the direction of illumination constitutes the determining factor, at least in certain instances.

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[25] Guttenberg, H. von., Studien über den Phototropismus der Pflanzen. *Beitrage z. allgem. Botanik,* 2, 1922.

If, as previously described,[26] the minute one-celled spores of the liverwort *Anthoceros* be sowed on the horizontal upper surface of porous, unglazed, clay plates standing in a suitable nutrient solution, under suitable illumination, they will presently germinate. Their subsequent growth, while influenced by the quantity of light,[27] will be determined, as is the duration of growth and of cell division in the hypha-like but green plantlets which come from the spores, by the direction from which light falls upon them. If the light come horizontally from a window upon cultures in glass dishes covered with opaque lids, the plantlets will spread out at right angles to the incident rays, that is, parallel with the window, forming rhizoids only on the side away from the window, the darker side. On the other hand, if cultures otherwise identical in origin, composition, age, position, and every other respect are revolved on vertical axes, as may be done on a suitable clinostat, so that they will receive light upon all sides in succession and in approximately equal amounts, the young plants will not spread out, becoming dorsi-ventral and standing parallel to the window, but will be obconical or vasiform, erect, circular in cross section, with rhizoids on all sides of the circular base. Refraining from any theorizing as to the primitiveness of radial structure,[28] and confining ourselves to what the experiment actually shows, we see that by making the one change, namely in the direction of illumination, the plantlets growing from the one lot of spores will be dorsi-ventral, as they always are out-of-doors, growing on flat or sloping soil, and receiving light almost entirely from above; or they will be radial if they receive light on all sides in succession. Furthermore, these radial plants will be so normal that they will contain, like their dorsi-ventral fellows in cultures unrevolved, the colonies of *Nostoc* which *Anthoceros* is well known to harbor. In circular cross sections (not triangular), in radial structure, in forming rhizoids on all sides of the rounded base, and in similar surface on all sides, these plantlets on the turntables have completely reacted to the formative influence of the direction of illumination; but so also have the dorsi-ventral plantlets of the otherwise identical but unrevolved cultures.

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[26] Peirce, G. J., Studies of Irritability in Plants: the Formative Influence of Light. *Annals of Botany*, 20, 1906.

[27] Goebel, K., *Organographie der Pflanzen*, 2te Aufl., 1ste Theil, p. 450, 1913.

Without going into similar detail it may be said that corresponding experiments upon certain usually dorsi-ventral marine algæ show that these plants also owe their dorsiventrality to the direction from which they receive light.[29] No experiments have yet been made employing constant illumination of cultures rotated on vertical axes so that they are equally exposed on all sides in succession to light coming approximately horizontally. The experiments on turntable cultures of germinating fernspores in daylight produced prothalli which bore archegonia, antheridia, and rhizoids equally on both sides, but the prothalli were as broad and thin as usual, though crinkly instead of flat or slightly curved.[30] As recognized by Pfeffer,[31] unless illumination is constant, there will occur at the end of each period of illumination, whether daily or oftener, an unbalanced stimulus, the effect of which upon a sensitive organism may be profound. Only experiment with the constant illumination now available will reveal the facts of the matter. Meantime, however, one is entirely justified in recognizing that the direction of illumination may profoundly influence the form of living organisms.

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[28] Goebel, K., *Organographie,* etc., p. 484.

[29] Peirce, G. J., *loc. cit.*

The directive, as distinct from the formative, influence of light, is matter of common observation. Stems generally turn toward the light; leaves generally spread at right angles to it, their upper surface facing the light; roots commonly turn away from the light and thereby tend to place themselves in normal relations to gravity (see pages 248–260). Many motile animals and plants move, by swimming or otherwise, toward the light or away from it, according to its intensity or composition. Bending or turning in response to light is termed *phototropism* (*heliotropism*), locomotion to or from light is called positive or negative *phototaxis*. The stimulus may be the same in intensity (quantity) and composition, but the response by different organisms, as well as different organs, may not be the same. There are organs and organisms which, because they give no visible response to exposure to light by bending or moving, seem not to be sensitive to it; and there are organs which furnish exceptions or contradictions to the general statements recorded above. Thus we find in the hypocotyl of the mistletoe — *Viscum*, *Phoradendron*, and *Arceuthobium* — stems which turn away from the light and therefore are negatively phototropic; and the petioles of the cotyledons of the California buck-eye (*Aesculus californica*) are probably negatively phototropic as they certainly are positively geotropic. Many roots appear quite indifferent to light, but those of *Allium sativum* are said to be positively phototropic. Most hairs are indifferent, but the rhizoids forming on the shaded side of fern prothalli and of the thallose liverworts grow away from the light. A considerable number of plants have pendent or erect leaves, similar in structure on both sides. It remains to be seen how much these positions are reactions to light and to what extent they are controlled by the water relations (transpiration, etc.) of the plants. Many of the experiments on phototropism have been conducted upon plants kept for a time in the dark. They are therefore deficient in chlorophyll, as compared with normal individuals of the same species; but many fungi, always devoid of chlorophyll, exhibit phototropism.

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[30] Peirce, G. J., *Studies of Irritability in Plants: the Formative Influence of Light.* Dudley Memorial Volume, Stanford University, 1913.

[31] Pfeffer, W., *Pflanzenphysiologie,* 2te Aufl., 2, 182, etc., 1904.

Positive, negative, and transverse phototropism (plagiotropism), and positive and negative phototaxis are seen, then, to be reactions of living cells, presumably their protoplasm, and certainly independent of color, to the stimulus of light, either to the direction of light, or to the differences in the amounts of light upon different parts. What the effects of light are upon the protoplasm, its constituents or contents, still escape determination. Working hypotheses at best represent our conceptions. What may be called the pressure of light, that is, the striking of ether waves upon the living cell (or upon any other given object) may be conceived to produce effects if this pressure is of such nature as to be effective, and if it is not offset by other and perhaps opposite pressure.[32] Temperature changes by the incident rays of the lower end of the spectrum might be conceived to affect the protoplasm, but it is known that seedlings exposed to one-sided illumination by rays mainly red, or infra-red, do not bend toward the light. On the other hand the blue, violet and ultra-violet rays at the upper end of the spectrum are shown by similar experiment to be the ones which stimulate the plant to turn toward the light. There are probably many light-sensitive substances, enzymes among the number, in living cells. These substances may be conceived to be so affected by the photochemical rays that their rôles in the metabolism of the cell are altered. But intra-cellular photochemistry is still unable to furnish any definite answer. Further, the influence of photochemical or other rays upon the permeabilities of the cytoplasmic membranes, a subject beginning to be worked upon,[33] may be considered as also involved in both growth and movement. The whole subject is open to speculation, theory, and experimental research. Till the last is accomplished one can only guess as to the actual effect of light upon living things.[34]

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[32] Chmielevsky, V. O., Phototaxis and the Pressure of Light. *Annals of Botany*, 38, 1924.

We come, then, to consideration of light as a directive stimulus. Motile organisms, both plant and animal, are generally sensitive to light. Sperms are said not to be; at all events they are clearly much more sensitive to chemical stimuli. Other bodies, such as the motile spores of fungi, which contain no chlorophyll, may be attracted by light; but the most striking examples of phototaxis among plants are afforded by the motile unicellular algæ or by the zoöspores of other algæ, although filamentous algæ, such as *Oscillatoria* and *Nostoc*, which are themselves motile, are definitely directed by light.[35]

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[33] Becking, L. B., and Gregersen, M. I., The Effect of Light on the Permeability of Lecithin. *Proc. Soc. Exp. Biol. and Med.* 22, 1924. Brooks, S. C., The Effect of Light on the Permeability of Lecithin. *Science*, 61, 1925.

[34] Becking, L. B., *Radiation and Vital Phenomena.* Utrecht, 1921.

[35] Pieper, A., *Die Phototaxis der Oscillarien.* Diss. Univ. Berlin, 1915.

In bottles or other circular vessels of colorless glass suitably lighted, the phenomenon of phototaxis among the algæ may be very strikingly exhibited, the algæ in the water congregating on the side toward the light and also on the side directly opposite the light. Measurements show that there are two parts of the liquid in a round bottle which receive more light than the rest, namely the part toward the window (or other source of light) and the part directly opposite. Ordinarily these two parts are not lighted to excess, although they may be deliberately or by accident; and they are generally the regions of most nearly optimum illumination. If the light be made more intense than the optimum at any point, one will see the motile organisms moving away to less lighted spots. Thus they may accumulate on the sides of the bottle instead of against the front and back. One may thus concentrate and collect the algæ dispersed through a volume of liquid, but ordinarily there is no further separation possible. In my laboratory, however, the two predominant algæ in a concentrated brine from a salt and magnesia works separate from each other on exposure to moderate illumination, the individuals of *Dunaliella viridis* congregating against the wall of their glass container on the side toward the light, while *D. salina* collects on the somewhat less brightly lighted side opposite. The behavior of these motile algæ finds its parallel in the behavior of other living things, which seek the degree of light most agreeable to them. As will be shown later, the position of these and other organisms at any one time represents the resultant of several or many influences, of which the direction and intensity of illumination is one, but of which oxygen is certainly another.[35a]

The position of the chloroplasts in the chlorophyll containing cells of many plants changes, as does the position of the motile algæ, according to the direction and intensity of illumination. Presumably the wave-lengths will also influence the position of both algæ and chromatophores, though this may well be further studied. The movement of the single plate-like chromatophore of *Mesocarpus* or *Mougeotia,* for example, of the small and numerous chromatophores of other filamentous algæ, and of the chloroplasts of more massive plants, though probably accomplished by the same means, do not necessarily lead to identical results. The positions of these organs within the cell itself is necessarily various, for manifestly adjacent cells or adjacent filaments may so shade a given cell or filaments that it may escape the full effect of the light. In all of these, too, the natural illumination of the plant and of its chlorophyll-containing cells may not be like that of the experimental material. One may therefore take the extensive work of Senn [36] as a starting point for further experiment under other conditions of greater natural illumination than those of Central Europe; but at the same time one may question whether the change of place of chromatophores in the living protoplasm of cells is altogether comparable with the locomotion of motile cells immersed in water.

[35a] See J. Buder, Zur Kenntnis der phototaktischen Richtungsbewegungen. *Jahrb. f. w. Bot.*, 58, 1917–19.

The phototropisms of roots, stems, leaves, and flowers are similarly influenced by the other factors of their environment. It is often necessary, therefore, to employ means such as clinostats for offsetting these other influences in order to distinguish the effects of light itself. In considering the directive influence of light, therefore, one must be certain that the directive influence of gravity, for example, is so firmly controlled that it does not confuse or otherwise impair the results of experiment.

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[36] Senn, G., Weitere Untersuchungen über Gestalts- und Lageveränderungen der Chromatophoren. *Zeitschr. f. Botanik,* 11, 1919. Gestalts- und Lageveränderung der Pflanzenchromatophoren. Leipzig, 1908.

So long continued and extensive have been the studies of the directive influence of light upon motile and growing plants that an elaborate and exact vocabulary has been developed in this field also. Whether the exactness of vocabulary is approached by exactness of knowledge is so open to question that one is justified in doubting the value of exact terms applied to extremely plastic living organisms. The exactness and uniformity of operation of even complex machines is very different from the universally recognized individuality of all living things. So a presentation time, reaction time, latent period, quantity of stimulus, quality of stimulus, and other details have been distinguished; but it is significant that among the figures of most of these from the same group of individual plants there is very considerable variation, and that different authors working on the same species, but undoubtedly on different strains and under different conditions of aeration, etc., agree only approximately if at all. The attempts to make biology an exact science, and to transform its vocabulary to one quantitative and pseudomathematical, admirably illustrate the inexactness and independence of operation of living organisms.

Many theories, clothed in more or less technical terms, have been advanced in explanation of the stimulating effect of light upon living protoplasm and living organisms. Critical review of these may be found in the writings of Blaauw[37] and of Koningsberger,[38] but it is not now possible to reach an adequate explanation of how the living cell and the living organism are actually (chemically and physically) affected by light.

[37] Blaauw, *l. c.*

[38] Koningsberger, *l. c.*

Changes in the permeability of the cell-membranes[39] and in the nature and rate of the intracellular chemical reactions, may readily be conceived on the basis of what is already known, but this is all very incomplete. These may well be regarded as working hypotheses, to be tested and abandoned, or subjected to modification and further testing as occasion may make desirable. Meantime, open-minded observation and experiment are indicated as the means of ascertaining these as well as the other facts of life.

In addition to the influence of light upon the form, structure, direction, and other features of the growth and behavior of plants, certain movements are induced by light which are not classed with either the formative or the directive effects. These are changes in position, involving changes in direction in many instances, accomplished by growth or by changes in turgor. Various authors[40] have attempted to distinguish these movements in response to stimulus from those previously discussed. The label applied to the movements apparently definitely directed by light, gravity, etc., is *tropisms*. These are said to be executed by radial structures and their direction determined by the direction from which the stimulus is received. The other movements are called *nasties*, of which photonasty is perhaps the most familiar, but with which should be coupled the response of tendrils and of the tentacles of *Drosera* to contact, *thigmonasty*, as previously described (pages 268 ff.); the *seismonasty* of such "sensitive" plants as *Mimosa* (pages 275 ff.); and the *chemonasties* to be described later (pages 333–349). But if this be the case one wonders about possible *geonasties* and what the fundamental difference is between geotropism, positive and negative, and geonasty, epi- and hypo-, which carry roots and stems respectively down into the soil and up into the air. When one looks through the list of plants executing nastic movements one sees that, in many instances, the movements are repeated, but so are the conceivable stimuli; that the reaction takes place in one direction only, regardless of the direction or side of reception of the stimulus, but this may be due to structural reasons; that the reaction takes place whether the stimulus be local or entirely general; and that the reaction may not take place at all unless the general condition be favorable at the time of stimulation. Other questions will suggest themselves as we consider individual instances.

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[39] Becking, *l. c.* Dixon, H. H., Variations in the Permeability of Leaf Cells. *Sci. Proc. Roy. Dublin Soc.*, 17, 1924.

[40] See Benecke-Jost, II, 362 *et seq.*

Many plants produce, in nature as well as in cultivation, flowers which open in the morning and close in the late afternoon or early evening. Some of these have been carefully studied by the masters,[41] but many more have not. In the spring landscape of California the poppy (*Escholtzia californica*) opens its orange-colored single flowers on five or six mornings in succession, while the magenta blossoms of redmaids (*Calandrinia caulescens*) open only once. Neither will open, no matter how bright the sunlight, unless the air be warm enough, though the difference of a degree or two at the critical temperature will determine whether the flowers open or remain closed. Similarly they will close on a warm afternoon as the light fails toward sunset, but they will close earlier if the air chills in advance of the decrease in light. These blossoms, then, execute thermonastic or photonastic openings and closings, a *Calandrinia* flower opening at best only once, an *Escholtzia* blossom opening five or six times. The opening and closing of these flowers is effected by the unequal growth of the outer (lower) and inner (upper) sides of the petals, the inner, upper, less lighted and very commonly somewhat warmer side growing faster in the waxing light and bending the petal open. On the other hand, the outer, lower, less lighted and at first perhaps somewhat warmer side growing faster in the waning light bends the petal upward and closes it with its fellows. These petals are dorsiventral organs, broad and thin, with a skeleton of vascular bundles which determines the line of least resistance to change in form. Tissue tensions produced by different rates of growth under the stimulus of light or of warmth accomplish the bending along this line. The epinasty which opens the blossom follows the stimulus of light in sufficient warmth, but will not take place in sufficient light without due warmth, nor at a suitable temperature without bright light. The hyponasty which follows in falling temperature or in waning light, undoes, reverses, the result of epinasty; but these cannot be compared with reversible chemical reactions, for there is an increasing residue in the increasing size of the petals. This is growth, stimulated by light, directed or determined as to direction by the structure of the petals themselves.

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[41] See Pfeffer's studies of tulip, crocus, etc., in his *Physiologische Untersuchungen.* Leipzig, 1873.

Corresponding with the colored blossoms which open by day, though at very different times in the day, for example, morning glory and four o'clock (*Ipomœa purpurea* and *Mirabilis Jalapa* respectively), there are flowers, mainly white, which open only as the light fades, closing as the day comes. The mechanics of opening and closing appear to be similar, namely more rapid growth of the inner face of the petals, forcing over the slower growing outer side and opening the blossoms; and conversely the more rapid growth of the lower side, the bending of the upper side, and the closing of the blossom. In these night bloomers also there is not only the increase in the rate of growth of the upper and the lower faces but the whole petal grows, the amount of growth varying with the temperature, humidity, etc., as well as with the illumination.

The phenomenon imaginatively and mistakenly called sleep movements (nyctitropic or nyctinastic movements) is exhibited more conspicuously by leaves than by flowers. In many of these the movements cease when the parts attain their growth,[42] while in others, those provided with pulvini, movements may be continued long after. In all cases the movements of opening and closing the leaves occur only when the air is warm enough. Leguminous plants and species of *Oxalis* offer the most familiar examples. In different cases in these, and other families, the leaflets are closed together either by being raised or by falling; in either case the increase or decrease in turgor of the cells of the pulvini of the separate leaflets brings about the change in position of the leaflets themselves. The stimulus, whether resulting in changed permeability of the cell-membranes or in changed rates of metabolic processes, results in pushing the leaflets up together, so that their upper surfaces touch, or in letting them fall so that their lower surfaces are proximate. The changes in the turgor of the pulvini, thus lifting or lowering the leaflets, are not changes in growth, are not accompanied by growth at all, and therefore are not properly called nasties in the strict sense of the term. Similarly one may question the general hypotheses as to the object or advantage of the closing of leaves with the change in light. Reduced transpiration or chill or conspicuousness, while resulting from the " sleep movements " of leaves, are not necessarily of sufficient importance to convince one that they are ends in themselves. They may well be incidental advantages.

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[42] See Pfeffer, W., Untersuchungen über die Entstehung der Schlafbewegungen der Blattorgane. *Abhandl. d. K. Sächs. Ges. d. Wissenschaften,* 30, 1907. Wiedersheim, W., Studien über photonastische und thermonastische Bewegungen. *Jahrb. f. w. Bot.* 40, 1904.

On the other hand, the various features of the behavior of plants known to be influenced by light are also influenced by the usual periodicity of light. There are the periodic phenomena just described, of the opening and closing of flowers and of foliage, plainly related to periodic changes in light, and induced in part by rhythm established in the plant by the rhythm in its illumination; but that there are other and more important rhythms in the behavior of plants, due to rhythmical illumination, is also probable. This can be clearly demonstrated, however, only when plants are cultivated from seed to seed under constant, uniform, adequate illumination, with due attention to constant temperature, humidity, and supply of food materials; and also when, conversely, in place of complete lack of rhythm, rhythm is deliberately established and maintained. Comparison of the results of these two sets of experiments should show whether some of the phenomena called periodic movements are any more than reactions to given quantities of stimulus, ordinarily furnished, to be sure, in nature at regular intervals. But the periods of germination, vegetative growth, bloom, and fruiting regularly recurring in nature may well be much more than accidentally connected with the regularly shifting seasons. They may bear quantitative relations to the amounts of solar energy available or accumulated at different stages in the life of the plant. Thus the phenologist, professional and amateur, knows and records the blossoming times of the plants of his interest over a period of years, and we all recognize that one season is "early" and another "late," facilely accounting for this as due to more than the usual warmth or to untimely cold, although reflection convinces us that light, heat, moisture, and other factors are all involved in the behavior of living organisms. The periodic movements, though like other periodic phenomena, should not continue, without much new evidence based on careful experiment with the extended facilities of to-day, to be regarded as the expression of rhythms greatly prolonged beyond the period of stimulation.

In this connection one may also speak of the so-called autonomic or endonomic movements, very striking in certain quite unusual instances, very inconspicuous and perhaps merely incidental to more important phenomena in all the rest. Thus the so-called telegraph plant, *Desmodium gyrans*, moves its leaflets and its compound leaves themselves with such speed under favorable conditions of temperature and humidity as to be plainly visible to the unaided but attentive eye. It is a phenomenon the importance and significance of which in Nature may well be conceived to be in inverse proportion to its extraordinary and unique character. If the advantage of rapid movement were considerable, one would naturally expect more than one species of plant with compound leaves to have developed the power and the practice of movement of its leaves and leaflets.

On the other hand the phenomenon of circummutation (as described by Darwin,[43]) exhibited by the roots, stems, and leaves of land plants, is a very general one. Under natural conditions, in which light and darkness regularly succeed each other, with consequent changes in temperature, humidity, and perhaps also intracellular conditions as well, both below ground and above, it is very possible that stimuli are so regularly periodic or progressive that the course of the reactions corresponds. The circummutation of root, stem, and leaf is apparently effected by progressive differences in the rates of growth in successive parts of these multicellular organs; but the movements of the filaments of *Oscillatoria* and *Spirogyra,* which are septate filamentous algæ, and of *Vaucheria,* which is not septate, show that the tensions upon which the bendings depend are not confined to tissue systems, but occur in protoplasm as well. The formation of buds in the summer and fall, and their opening in the following spring, are due to the succession of hyponastic growth of the scales and other parts followed, after an interval of cold or drought, by the epinastic growth, and still later by the balanced growth, of the same parts. In this succession of nasties, and possibly also of tropisms, and of other phenomena caused by changes in turgor as well as by growth and tissue tension, there is nothing to show that these periodic and apparently autonomic or endonomic movements are not the consequences of perfectly definite if at the moment hidden influences acting as stimuli upon the living organism and its component cells.

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[43] Darwin, C., *Power of Movement,* etc.

The act of fertilization, which, as we shall presently see (pages 344 ff.), confers a chemical as well as mechanical addition and stimulus to the egg, is followed by movements and other changes in the pistil and other parts of the flower and fruit. These movements and other changes are not only subsequent to fertilization but due to it; and having already seen (pages 305–314) that blooming is a consequence of illumination, we are the more ready to recognize that the changes following fertilization are not autonomous but are the sequelæ of sequelæ of reactions to stimulus.

The re-study of autonomic, periodic, nastic and tropic movements, and of the possible formative effects of light and other stimuli, is now amply justified by the improved means of control of conditions and influences under which plants live.

The Influence of Heat

In previous pages[44] various aspects of the relation of heat to life and to the activities of living organisms have been considered.

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[44] See pp. 6, 7, 8, 76–7, 181–3, 193.

No other factor of the environment acts as plainly both as a condition and as a stimulus to the various and respective activities of living organisms. While it may not be absolutely known why certain chemical reactions take place only when the temperature is above a certain point, and go on more and more rapidly as the temperature is raised, the fact is familiar. It is natural to assume that there are analogous reasons for the relations of living organisms and their vital processes to temperature. There are minimum, optimum, and maximum temperatures for organisms and for their vital processes individually considered. Below the temperature of 0° C. extremely few organisms are active though, as has been shown already,[44] many organisms can survive this and even much lower temperatures, if not too prolonged. Few organisms can survive temperatures approaching that of boiling water, 100° C., and many are killed by much less heat. These are the limiting conditions of active life, and temperature must be considered as one of the "limiting factors" of life.[45] Between the temperatures of boiling and freezing lie those temperatures which are the optima for specific organisms and their individual functions. The optimum temperature for the whole organism is not necessarily the optimum for the processes which it may carry on. The organism may grow most rapidly at a temperature which is above the optimum for reproduction; its oxidative metabolism may take place more rapidly if the temperature is raised above the optimum for growth; but if the humidity, the water and carbon dioxide supply, and the illumination be raised at the same time as the temperature, a new series of optima may be established. We must recognize, therefore, that temperatures are minimum, optimum, and maximum according to the prevailing balance of the other factors of the environment. The interrelations of these factors, the correlation of living organisms to them, and the coördination of the different functions of the organisms to each other, form a complex, the intricacy of which it is very difficult adequately to conceive. It is obvious, however, that if one attempt to isolate one factor or another for consideration, one will necessarily fail either by not eliminating the other factors, or by subjecting the organ or organism to correspondingly unnatural conditions and to consequent undue strain. One cannot eliminate all heat, for if one did, all processes would stop. A certain amount of heat, then, constitutes a condition for active living.

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[45] Blackman, F. F., Optima and Limiting Factors. *Annals of Botany*, 19, 1905.

The supply of this amount of heat, constituting a condition for active living, is not constant but periodic over the major fraction of the earth's surface, in summer and by day greater, in winter and at night less. Associated with this periodicity in heat furnished to the earth by the sun is the rhythmical behavior of many plants and animals. It should not be inferred, however, that this rhythmical behavior is the consequence of the periodicity of heat supply only but of all the other periodic agencies composing the procession of day, night, and the seasons (pages 296–329).

But just as, periodically, active life is possible and impossible because of the temperature, acting both as a condition and as a limiting factor, so periodically heat acts as a stimulus also, formatively or directively as the case may be, the increasing warmth of spring and the temperatures of summer stimulating growth both quantitatively and qualitatively, and regulating the form as well as the position (direction) of organs and organisms. Thus in a certain swimming pool near this University the growth of algæ (*Chlamydomonas*) was slight at a temperature of 15° C., but the slight increase of 2° C. which took place in consequence of clear sunshine was accompanied by such an increase in the number of algæ at the end of three days as to cause the water previously clear for three months to be so clouded that one could not see the bottom ten feet below the surface.[46] In the case of water and water plants, however, one must bear in mind the effect of the temperature of the water upon oxygen and carbon dioxide content, upon consequent alkalinity, neutrality, or acidity (P^H), upon density, and possibly upon other things of no less importance (pages 45–46 ff.).

The formative influence of heat is by no means clearly marked. While it is obvious that trees of the tropics and subtropics do not attain normal dimensions when cultivated elsewhere, there are so many factors involved besides heat that one dare not attribute this familiar fact to heat alone. *Eucalyptus globulus* and *Sequoia gigantea,* grown in pots in the greenhouse in Cambridge, Massachusetts, or Leipzig, Germany, attain their well-known proportions only in Australia and California. The differences in size and form of the leaves and other parts of tropical and temperate trees are doubtless due in part to the formative effects of heat, but humidity as well as other factors are apparently more influential.

On the basis of extended observations, both of marine algæ and of land plants, Setchell[47] has expressed the conviction that " the temperature variable is the one controlling anthesis, not the moisture variable or the hours-of-daylight variable," that waves of bloom occur in months " when the mean maxima and the mean minima of temperature for the month are approximately 5° C. apart from one another," and that there are " definite points of critical temperature for anthesis " at intervals of 5° C. between 5° and 30° C. Both the conclusions and the observations are sufficiently interesting and important to justify the testing of the observations by extending them to conditions very different from those prevailing in the sea and on the west coast of the continent. While critical temperatures are familiar enough in physical chemistry, one may wonder whether they or the amounts of energy which they indicate are the essential factors. Only careful investigation of both possibilities can determine the point.

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[46] Observations on the Swimming Pool of Clarence Walter, Esq., Atherton, California, on March 16 and 19, 1925.

[47] Setchell, W. A., Temperature and Anthesis. *Am. Journ. Botany,* 12, 1925.

As to the directive influence of heat there is an abundance of contradictory evidence, and the matter must be left to the curious to settle. It used to be stated that roots would grow in cool soil toward the warmth radiating from buried steam pipes. While no one will question that roots will grow faster and therefore larger in the same time in soil which is warmer than in soil too cool, experiment has not yet clearly shown that there is positive *thermotropism*[48] of roots. Thermotropic bending of branches of trees, hard to distinguish from bendings due to turgor changes, are claimed as well as the movements of other aerial parts of plants. In all of these instances, however, the directive stimulus of heat has importance and significance quite secondary to the importance of heat as a condition for active life.

The Influence of Water and of other Substances

The presence of a minimum amount or proportion of water in the body and in the environment has been shown in the foregoing pages[49] to be indispensible to active living, and the presence, in suitable proportions, of compounds of at least ten chemical elements[50] has also been demonstrated as necessary.

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[48] Collander, R., Der Reizanlass bei den thermotropischen Reaktionen der Wurzeln., *Ber. d. d. bot. Ges.*, 39, 120, 1921.

[49] See pages 10 to 41.

[50] See pages 44 to 132.

Water and certain other substances are among the conditions of life. Just as a certain amount of heat (see pages 329–333) must be present or no chemical change of any sort will take place, so there must be a minimum amount of water or none of the metabolic processes of the living organism can go on. Similarly there are the indispensable minima of other necessary substances. Amounts of these substances above the minimum requirements influence the behavior, external or internal, of living organisms. These influences may be regarded in many instances as being evidently and simply direct, while in other instances the results following their presence cannot be described as directly due to them. As in many other instances, it is necessary, at least at present, to conceive that the presence of water, or of any other substance, beyond the minimum proportion, may exert an influence upon the physical or chemical conditions or changes within the body. One must therefore entertain the idea that many substances constitute not only conditions for existence, but also stimulate the living organisms, which respond, thus revealing the formative or directive influence of the particular stimulus.

It may be conceived to be the peculiar province of the ecologist to consider anything more about water and its influence upon plants than has already been discussed in the foregoing pages under photosynthesis, transpiration, etc. or will be discussed under the term hydrotropism; but plant ecology, when it is scientifically anything more than taxonomy with geographical emphasis, is the study of certain parts of plant physiology. The reactions of plants to the distribution of water in soil, air, and mass, and to the other components of soil, air, and fresh and salt water, are physiological, to be treated, if one choose, with laboratory exactness or with loose largeness. Thus the occurrence of thin, large, moist leaves on plants living in comparative shade in damp situations, of thick, small, dry or leathery leaves on unshaded plants in dry places, and a certain fleshiness in plants of marsh and bog, are facts of geographical distribution; but these facts represent the reaction of the individuals of these species to these particular circumstances, and laboratory experiments confirm correct ecological inference.

On the Pacific Coast there are included in the flora two seasonal types of flowering plants, best illustrated perhaps by the short fleshy "miner's lettuce" (*Montia*) which thrives during the rainy season of high soil moisture, high humidity, and low evaporation, and by the tall, slender, dry "tar weed" (*Hemizonia*). At the same time that there are pronounced differences in soil and air moisture, it goes without saying that there are also consequent differences in temperature, illumination, water loss, water absorption, and water conduction through the stem, all of which have their own formative influence upon the organism.

Especially where there is ordinarily no excess of water over current seasonal requirements, the foliage of deciduous trees varies from year to year particularly in the size of the leaves. In the current spring (1925) the new leaves coming out on the live oak (*Quercus agrifolia*) have an area 25–50% greater than those of 1924. It remains to be seen whether in thickness, degree of cutinization, dry weight, and other characters the individual leaves and the total mass of foliage of the live oak will differ materially at the end of the dry season of 1925 from that of 1924. The point to be recognized now is that in the complex of formative stimuli operating upon the rapidly growing leaves of this tree one may distinguish the immediate effect of water, both the water in the soil and the water in the air. The rainfall of this year, about 17 inches, is more than double that of last year, and the distribution of the rainfall during the season has been much more favorable this year than last. The result is leaves at least equal in number to those formed last year, and greatly exceeding them in size. One should realize that the shape, size, thickness, texture, cutinization, and vascular supply of each individual leaf are the resultant of heredity (substance) and of circumstance, and that under the latter head must be included water supply and water loss, illumination and its effects on photosynthesis and transpiration (pages 55–150), and the action of gravity (pages 235–261). Laboratory and greenhouse culture show the direct connection between water in soil and air with these features of this and last year's foliage. It is common experience in this region that Windsor bean (*Vicia faba*) plants grown in the open and under glass differ markedly in the character of the leaves, those out of doors having leaves of the usual size and thickness with the stomata mainly in the epidermis of the under side, while those under glass at much the same temperature and illumination but considerably higher humidity have stomata in equal numbers on both sides of the rather larger and more fleshy leaves.

The temporary checking of growth and the reduced foliage in transplanted plants commonly observed [51] must be ascribed to the reduced supply of water by the amputated or wounded roots. Water, in such instances, is *a* or *the* limiting factor,[52] whether we conceive the effect to be due to insufficiency of water for metabolic or for mechanical purposes.

If, however, we inquire further and more deeply in regard to water as a formative stimulus, comparing land and water plants [53] as to their mechanically strengthening and supporting tissues, as well as those for absorbing water and other food materials, we recognize at once that the difference in the buoyancy of air and water entails certain necessities or exemptions respectively. Thus the buoyancy of fresh water is seven hundred times that of air, the buoyancy of sea water somewhat higher, and the supporting skeletons of water and land plants correspondingly developed. While the tensile strength of the great brown kelps is very great,[54] and correspondingly great in *Fucus* and even smaller seaweeds, their bearing or supporting strength is slight. As in so many other instances, however, the buoyancy of water is an offset to the downward pull of gravity, and each aquatic organism is therefore subject to the formative influence of both (pages 235–247).

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[51] Copeland, E. B., A biological note on the size of evergreen needles. *Bot. Gazette*, 25, 1898.

[52] Blackman, *l. c.*

[53] Peirce, G. J., A Comparison of Land and Water Plants. *Pop. Sci. Monthly*, July, 1903.

The locus and the ease of water absorption by any living organism are also greatly influenced by water. Thus, for example, experimental studies as well as the observations of Goebel[55] and many others on the results of continual immersion in water, life on the surface, and complete immersion in air, both continually and periodically, show that the means for the absorption of water and dissolved substances (oxygen, carbon dioxide, mineral salts), and the means for controlling outgo, are developed with great exactness according to the formative influence of water.

Furthermore, the effect of the quantities of water required to be absorbed and moved rapidly greatly influences the formation of spring and summer wood, the cuticula of leaves, the number of leaves persisting throughout the summer, and even possibly their color.[56]

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[54] Cannon, W. A., Note on the Bladder Kelp, *Nereocystis Lütkeana.* Torreya, 1, 1901.

[55] Goebel, K. von., *Organographie der Pflanzen.* 2te. Aufl., I, 21, 1913.

[56] The dryness of "autumn" leaves is well known, and the production of the disease known as "red belt" is directly connected with inadequate transfer of water to the leaves affected.

The indirect but no less important effect of water either as translucent vapor or as more or less opaque cloud upon the organisms which would otherwise enjoy more complete solar irradiation is only imperfectly recognized. As already indicated (pages 308–311), water in the air acts as a damper upon the passage of sunlight. Both the total amount of solar energy and the wave lengths of the rays reaching the land or water surface are regulated by the amounts and the form of water in the air, and plants and animals behave accordingly.

Plants living in soil or in water are profoundly influenced by other substances than water. If other than mechanical effect is produced by these other substances, they act in solution in water. The composition, reaction, and density, therefore, of the aqueous solution, whether in soil or stream, are of the utmost importance. While this has long been known, there have been no convenient and exact means of expressing these qualities until comparatively recently. For these means we are indebted to the vocabulary of physical chemistry. This can be most clearly shown by discussing specific instances of the formative effects of different solutions.

In this region of alternating rainy and dry seasons, during which sunny days are not lacking to diversify the rains but in which rain falls only very exceptionally at any other time in the year than during the rainy season, one may very significantly trace the successive changes in vegetation both on the land and in the water. In addition to the fact that we have a rainy season flora and a dry season flora composed of annuals with corresponding characters (page 335), as well as those perennials which, like plants and animals between the tide marks, must adjust themselves to both sets of conditions, there is a regular succession of plants in the waters according to the changes occurring during the twelve months. This is clearly illustrated by an artificial lake on the campus of this

University. During the successive rainfalls of late autumn and throughout the winter the lake fills with a considerable body of quite soft water. This being a region of hard water, the Searsville Lake forms a marked exception in the spring. The water (pH 7.4) is somewhat turbid from silt. It is now occupied mainly by *Bacillariaceæ* (diatoms). As the season progresses, evaporation brings about the gradual hardening of the water (pH 8.0) and *Chlorophyceæ* predominate. At the same time photosynthesis, taking place actively in the upper two meters of the whole lake, in removing CO_2 during the day, is still further increasing the alkalinity (pH 8.6). In quiet water, unruffled by wind, a supersaturated solution of O_2 may result, the O_2 being conspicuously discharged on dropping a stone or thermometer or other heavy object into the water. On the other hand, during the night in these upper two meters, and throughout the twenty-four hours in the layers below, to which only faint light penetrates, there will not only be no accumulation of O_2 but on the contrary a decrease in it and a corresponding increase in CO_2. According to the depths, temperatures, etc., circulation tending to equalize conditions throughout the lake will or will not take place. *Cyanophyceæ,* tolerant of organic matter undergoing decay, predominate when the waters are warmest. That this succession is due to the changing condition of the solution rather than to times, seasons, or the nature of the organisms themselves, is shown by simultaneous cultures differing from one another only in respect to the composition and reaction of the solution.[57] Thus in a standard Knopp's solution reduced to a dilution of 0.04375% and so modified in different Erlenmeyer flasks of two liters capacity as to have a range of acidity-alkalinity from pH 5 to pH 9, there is found to be no growth in the solutions of maximum acidity and alkalinity when these are inoculated with mud from Searsville Lake, whereas in solutions ranging from pH 7 to more than pH 8 there is an increasingly abundant phytoplankton. In these cultures, as in the Lake itself, the diatoms predominate when and while the solution and the water, respectively, are most acid (or least alkaline), the green algæ following these as the water increases in alkalinity or, in the cultures, developing most abundantly during a gradual rise of the pH from neutral (7) to alkaline (8). On the other hand, the predominance of blue-green algæ (*Cyanophyceæ*) at higher temperatures coincides with their predominance in the tropics. Further studies of this relation in regard to the proportions of dissolved oxygen and CO_2 in the water are indispensable to definite understanding of this aspect of the succession in a pool or pond, as well as of the peculiarities of occurrence of this great group of organisms.

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[57] Scott, F. M., *Introduction to the Limnology of Searsville Lake.* Stanford University Publications, University Series, 1925.

While similar single changes in the environment cannot now be shown to be the predisposing causes of seasonal successions either in many of the organisms themselves which live upon the land, or in their behavior, yet the foregoing pages record certain examples among land plants. No doubt many more will become known as studies of this question are continued.

The geographical distribution of plants, while known to coincide among other things with certain conditions of moisture, is also connected with specific soil ingredients. Thus there are so-called calciophile plants, for example the grasses, and calciophobe, such as *Sphagnum* and certain pines, respectively plants growing on limey and on "acid" soils. In these cases it may well be questioned, however, whether it is the calcium ions as such, or the hydrogen or hydroxyl ions, in the soil and hence in the soil water, which exert the chemical stimulus to which the behavior of the plant is the response.

Experiment seems to show in these cases, as in the experiments with algæ cited above,[58] that neutralizing the natural acidity with sodium is as efficacious as with calcium salts. Furthermore, the balance of calcium, potassium, and magnesium salts, of iron, silicon, and other compounds, must be taken into account along with the acid, alkaline, or neutral reaction of the soil water.[59] A deficiency or an excess of one soil constituent apparently influences the ability of the living plant to secure, under the conditions, a sufficient amount of one or more of the others. Thus chlorosis (see pages 78–79) may be due to calcium or iron, potash or other deficiency, although one or all of these elements are present in the soil. One element may seem to "lock" another in the soil or the soil solution.

The extensive and painstaking studies of Cannon[60] on the behavior and on the environment of roots put us in possession of information and ideas in regard to the conditions of aeration and moisture supply in the soil which only his experimental work has furnished. Thus we see, for example, that the looseness or compactness of soil, leading to greater or less air content, and hence to corresponding oxygen supply, entails not only greater or less growth in length, size, and number of roots, and the relative depths to which they will penetrate, but also regulates the number and length of root-hairs. It has long been known that Indian corn seedlings, (1) grown on moist paper or cloth under a bell glass, (2) in dry loose gravel, (3) in wet heavy clay, and (4) in boiled water, develop respectively (1) a velvety "pile" of very many and long root-hairs, (2) many though shorter hairs, (3) few and still shorter hairs, and finally (4) very few and short hairs. This behavior of the epidermal cells of the young root is ordinarily regarded as directly related to the abundance and ease of absorbing water, the more the water the fewer and shorter the hairs, and *vice versa;* but if one reflect upon the physical principles involved in osmotic absorption of water and dissolved substances, one will see that there is hardly likely to be any deficiency of water in warm air of 90–100% humidity or any difficulty in taking water molecules from warm moist air into the epidermal cells of young roots. The differences, therefore, are in respect to the solutes rather than the solvent. The solutes fall into two classes, the gases O_2 and CO_2, and the mineral salts. The latter may be equally abundant in water, in soil water, even in atmospheric moisture,[61] but the proportions of O_2, if not of CO_2, in air and in the atmosphere of loose gravelly soil, are manifestly greater than in wet clay and in boiled water. The experiments of Cannon, therefore, in which the development of root-hairs is directly proportional to the amount of free oxygen in the soil, show the formative influence of this gas as distinct from, though complementing, the relation of the roots and root-hairs to water.

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[58] Scott, F. M., *l. c.*

[59] Gile, P. L., and Carrero, J. O., Cause of Lime-induced Chlorosis and Availability of Iron in the Soil. *Journ. Agric. Research,* 20, 33, 1920. Hendrickson, A. H., A Chlorotic Condition of Pear Trees. *Proc. Amer. Soc. for Hort. Science,* 1924.

[60] Cannon, W. A., Physiological features of roots with especial reference to the relations of roots to the aeration of the soil. Carnegie Institution of Washington, 1925.

Again, it is well known that plants of different species send their roots into the soil to and through very different levels. Alfalfa, for example, is said "to send its roots to water," even though this may be at considerable depth below the surface. This may be regarded as hydrotropism, and on a very large scale; but the relation of alfalfa roots to oxygen, and the proportions of oxygen at different depths, must also play a considerable part, along with geotropism, in regulating growth below the surface. This is indicated by the distribution of root tubercles. Root tubercles,[62] formed in consequence of infection with the aerobic soil organism, *Bacillus radicicola,* are more abundant in the uppermost few centimeters of soil; but the depths at which they are found, and their abundance, are directly related to the degree of aeration of the soil, the looser and better aerated the soil the more abundant the root tubercles.

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[61] Clarke, F. W., The Data of Geochemistry. *U. S. Geological Survey Bull.* 770, p. 56+, 1924.

The practice of manuring and of chemical fertilizing of cultivated soils, the behavior of living organisms, and of the earth's surface itself, result in the application of chemical stimuli to living plants. To these stimuli plants respond by growth, vegetative or reproductive, and by movement. The stimuli may accelerate or retard growth, or they may attract or repel motile organisms. If the acceleration or retardation is general the stimulus may be said to exert a formative influence, but if its effect is so local as to be followed by a change in the direction rather than in the amount or kind of growth, it is said to be directive. We have then either a change in the rate of growth or a change in the direction of growth, a tropism controlled by water (hydrotropism) or by other substances (chemotropism). And similarly there are the phenomena of hydrotaxis and chemotaxis.

From the foregoing it may be inferred that, at the present time, there are no such clarity of conceptions and completeness of knowledge of the facts of the influence of water and of other substances upon plants as are indispensible to even such impressionistic treatment as the foregoing discussions of the influence of the other factors of the environment. We must content ourselves, therefore, with acknowledging this condition, describing a few examples and showing the ample opportunity for both detailed and comprehensive work in this field.

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[62] Peirce, G. J., The Root-tubercles of Bur Clover and some other Leguminous Plants. *Proc. Cal. Acad. Sci.,* 3d Ser., Botany, 2, 1902.

The act of fertilization as shown by Loeb,[63] Wilson,[64] Morgan,[65] and many others consists in the combination with the egg of certain structural, mechanical units (chromosomes, genes, or other) and, in these and the cytoplasm, substances of incompletely known composition. The former, except as they may be the carriers of the latter, are more interesting to the morphologist and cytologist than to the physiologist: but the physiologist finds that while chemical stimulation may be followed by development to a certain point, the chemically stimulated egg fails to be self-operative beyond a certain early stage. Whether this is for lack of food or for lack of essential parts of the mechanism we do not now know, but it is evident that in the process of fertilization throughout nature we have growth, often many different kinds of growth, following the stimulation (and completion) of the egg by the sperm. This stimulation must be regarded as both chemical and mechanical, and the subsequent growth as an instance of the formative influence of other substances in solution in water.

Many roots, stems, sporophores, germinating pollen grains, and rhizoids have been described as exhibiting positive or negative hydrotropism, bending toward or from a source of water or water vapor. Since the classical experiments of Sachs,[66] so frequently repeated, it has been recognized that the vertically downward growth of the main root and the oblique or horizontal growth of its branches, are subject to modification by the unequal distribution of moisture, and of other substances, in the soil. Young and growing roots, other things being equal, will grow toward more water or water vapor, being positively hydrotropic. Root-hairs, pollen tubes, the hyphæ of many fungi, and perhaps stolons and rhizoms also, exhibit positive hydrotropism. On the contrary most stems and branches seem quite indifferent, only sporangiophores or sporophores being in general negatively hydrotropic. Thus the sporophores of *Mucor* and a considerable number of other fungi,[67] of *Fimbriaria* and other liverworts, and perhaps the flower and fruit stalks of many low herbaceous plants, turn away from the dampness of the substratum into the air. This turning, not necessarily coinciding with geotropic bending, may be instigated either by gravity or unequal distribution of moisture, but is modified by the other to such a degree that the final position of the organ is usually the resultant of the two.

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[63] Loeb, J., On the Nature of the Process of Fertilization, etc. *Amer. Journ. Physiology*, 3, 1899.

[64] Wilson, E. B., *The Cell in Development and Heredity*. 3rd Ed., 1925.

[65] Morgan, T. H., *The Physical Basis of Heredity*, 1919. Cowdry, E. V., and others *General Cytology*, 1924. Tischler, G., *Allgemeine Pflanzenkaryologie*, 1921–22.

[66] Sachs, J. von, Ablenkung der Wurzeln von ihrer normalen Wachs-

Plants of different sorts may be successfully grown very close together on the same area if they do not unduly shade each other and do not occupy the same soil levels with their roots. Thus, I found by accident that Monterey cypress (*Cupressus macrocarpa*) and Blue Gum (*Eucalyptus globulus*) will grow together for years, the horizontal roots of the latter overlying the spreading roots of the former.[68] Whether water or oxygen is the controlling influence in these

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thumsrichtung durch feuchte Körper (Hydrotropismus), *Arb. bot. Inst. Würzburg*, 1, 1872; *Gesam. Abhandl.*, 2, 971, 1893. Hooker, H. D., Jr., Hydrotropism in Roots of Lupinus albus. *Annals of Botany*, 29, 1915.

[67] Walter, H., Wachsthumsschwankungen und hydrotropische Krümmungen bei Phycomyces nitens. *Zeitschr. f. Bot.*, 13, 1921.

[68] McMurphy, J., and Peirce, G. J., Drought and the Root System of Eucalyptus. *Science*, N. S. 51, 1920.

cases I do not know; for without laboratory determination of the oxygen supplies and oxygen requirements of these two species their behavior out of doors is unexplained. The importance of these relations to the forester and the agriculturist and horticulturist are, however, obvious and deserve much fuller investigation.

Other stimuli than water and oxygen occasion chemotropic bending. The specific names hydrotropic and aërotropic indicate only special forms of the general phenomenon of sensitiveness to chemical influence and the power of reaction. The bending of the tentacles of *Drosera* in response to contact with a nutritious or otherwise suitably irritating (stimulating) object (page 117) is an example of chemotropism. So also is the growth of pollen tubes [69] into and through the stigmas and styles and toward the ovules, the eggs of which they may fertilize. The growth of the hyphæ of many parasitic fungi is similarly directed by chemical stimulus emanating from the prospective host plant.[70] The growth of the conjugation tubes of *Spirogyra* and its allies may be directed by chemical stimuli emanating from adjacent tubes which thereupon grow toward each other. But while the idea is entirely plausible, it has not been proved by experiments which have avoided all the difficulties inherent in the question.[71] On the other hand Hemleben [72] reports his observations of different species of *Spirogyra* both in nature and in cultures, and concludes that only those filaments and those cells conjugate which are in contact with each other. He would, therefore, eliminate chemotropism as directing the growth of the conjugation tubes; but unless he limits the stimulus to contact only (see pages 261–279) he must admit the possibility of what I have called above the formative effect of chemical stimulation. Owing to the smoothness of the *Spirogyra* filament, due to its gelatinous sheath, it is less irritating than rougher objects; but experiment has shown that it is none the less susceptible to contact stimulation (page 262). In any case, however, the much studied *Spirogyra* still offers this, among many, unanswered questions.

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[69] Lidforss, B., Ueber den Chemotropismus der Pollenschläuche. *Ber. d. d. bot. Ges.*, 17, 1899. Also Miyoshi, *Flora* 78, 1894.

[70] Miyoshi, M., Ueber Chemotropismus der Pilze. *Bot. Zeitung*, 1894.

[71] Haberlandt, G., *Die Sinnesorgane der Pflanzen.* Leipzig, 1909.

[72] Hemleben, Ueber die Kopulationsakt und die Geschlechtsverhältnissen der Zygnemales. *Bot. Archiv.* 2, 1922.

In the matter of pollen it is evident that the sticky, nutritious stigmatic surface on which a miscellaneous collection of pollen grains may find itself must consist of substances which check as well as others which permit or promote the germination and growth of the grains and tubes. The chemotropic growth of a pollen tube through the style to the ovary and an ovule of the same species may be coincident with the complete inaction of a pollen grain of another species. The conception, therefore, of growth-checking substances is as natural as that of growth-promoting compounds. The idea of such substances in plants is a very familiar one, whether they are called hormones (page 282), antibodies, or anything else: but the difficulty in proving the occurrence of such bodies is at present insuperable.

Turning now to locomotion directed by water, oxygen, or other chemical influence, exhibitions of chemotaxis are numberless, varied alike according to the organism and the medium or the circumstances. Thus a "slime mould," living upon a solid and indifferent substratum, may be stimulated to move in a definite direction by a stream of damp air of suitable temperature. If proper precautions are taken, the locomotion of the plasmodium toward the source of the stream will be recognized as positive chemotaxis, or more specifically hydrotaxis, due to the moisture and not to the warmth or oxygen.

In all such phenomena, care must also be taken to distinguish the influence of water *per se* from the *chemical* influence of any or all of the substances dissolved in it, and also from the effect of the *concentration* of any or all of the dissolved substances. There is in fact the phenomenon of sensitiveness and reaction to osmotic pressure, to which the names of *osmotropism* and *osmotaxis* have been given. It has indeed been suggested that hydrotropism and hydrotaxis are in reality exhibitions of negative osmotropism and osmotaxis. So far as I can see, however, the distinction has no further value than is directly implied by the terms.

Since the classic work of Pfeffer [73] there have been many studies of the influence of nutritious and other substances upon the direction of swimming of sperm cells, bacteria, zoöspores, etc. There have arisen from the many observations many working hypotheses and certain philosophical theories, such as the doctrine of "trial and error." [74] With these observations are involved others on what has been called *galvanotaxis* or *galvanotropism*,[75] for it is as yet by no means clear whether it is because of their electrical charges or because of their chemical affinities that stream or substance stimulates. We are, in fact, on a border line here, as yet unable clearly to formulate our conceptions of chemical, physical, and physiological phenomena and their causes. Either one must wait for the chemist and physicist to clear away the uncertainty or, using living organisms as well as lifeless materials, the physiologist may essay his own contribution to the foundations of science by attempting to determine the nature of chemical stimulus and physiological response.

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[73] Pfeffer, W., Locomotorische Richtungsbewegungen durch chemische Reize. *Unters a. d. bot. Inst. Tübingen*, 1, 1884. Jennings, H. S., *The Behavior of the Lower Organisms*, 1915.

[74] Loeb, J., *Forced Movements, Tropisms, and Animal Conduct.* Philadelphia, 1918.

[75] Zeidler, J., Beiträge zur Frage des Galvanotropismus der Wurzeln. *Bot. Archiv.* 9, 1925.

X

REPRODUCTION

Organisms differ from inanimate objects in forming parts of a generation which is the successor and usually the predecessor of its own kind. Whereas inanimate objects, like salt crystals, may be brought at will into existence for the first time, even the material of the crystals being made out of quite other substances, individual plants and animals presuppose parents and must themselves be parents unless the line of succession terminate with the living individuals. In this succession certain morphological features are involved which have been intently studied, amply described, and inadequately understood. They are the theme of the morphologists and of the biological philosophers. These morphological features involve results of the utmost importance to the individual, to the race, and to Nature: they are themselves the results of causes, the importance of which we may appraise, but which we recognize only imperfectly and inadequately.

In the foregoing pages attempts have been made to show that the behavior of plants, both vegetative and reproductive, represents the reactions of the living organisms themselves, composed of physical-chemical systems of diverse composition, to stable or transient influences, themselves the components of the vast complex of Nature. Reproduction, involving a single parent, or two, or even more (society), represents reactions to stimuli which we have discussed in the preceding pages. Even the formation of the reproductive organs and the activities of the reproductive elements, sperm and egg, are the results of the operation upon living organisms of the forces of Nature. As we discover that some of these forces are constant, uniform, unchanging, so we discover that substance corresponds to circumstance and is no more changing from generation to generation, age to age.

In these two facts, the continuity of substance and the continuity of circumstance, we have the gross outline of the phenomenon of heredity. Morphologist, geneticist, and physiologist, contribute in their own ways details of knowledge regarding the continuance of living things upon a persistent earth, regarding the changing of living things upon a changing earth, the development of individuals and the evolution of races.

By the continuity of circumstance or influence there comes about a continuity of substance, like begetting like. The living organism, a self-operating mechanism, is so under conditions which we know most imperfectly. It reproduces itself, conditions permitting, according to its kind. On preceding pages various influences — light, warmth, moisture, etc. — have been discussed in their bearings upon reproduction, upon the formation of reproductive organs, sperm and egg. We may return at this point to the question of what causes plant or animal to add the reproductive functions to those vegetative ones which it may have been carrying on for longer or shorter times. What causes a tree or a man which has grown for twenty or thirty years suddenly to blossom or to reproduce? When wheat may blossom at eight or ten inches, why should it generally wait till it is thirty or more inches tall? It has commonly been said that fruit and other trees about to die blossom prematurely or profusely, and that, in seasons of deficient rainfall, grain comes to head while the plants are relatively small. A certain amount of light is thrown on these questions by the painstaking work of Bakhuyzen.[1] Under the extraordinarily uniform conditions of his culture chamber — a dark room of almost constant temperature and humidity, in which powerful incandescent electric lights were operated continuously, and in which the plants, grown in washed sand, were supplied with the same culture solution throughout the experiment — wheat came into bloom when the ratio of water to dry substance in the plants fell to a certain point. After they began to bloom they ceased to grow in height, but continued to increase in dry weight. While this increase in dry weight was largely in the grains, the vegetative parts of the plants also increased somewhat in dry weight. The inference may be drawn, therefore, that blooming is due, not to the formation and accumulation of flower-forming stuffs (see page 309), or the stimulus of light (page 305), or the length of day (page 312), or the amount of photosynthates (page 311), but only to the ratio of water and dry substance. To draw any such or even any conclusion at this time would be repugnant to the author; but the experimental study of which this preliminary report is the first record is so full of promise that attention may well be called to it. For the conditions for the production of human food include the conditions of reproduction in plants.

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[1] Bakhuyzen, H. L. van de S., *Proc. Soc. Exp. Biol. and Med.*, 22, 1925. Consult the Food Research Institute, Stanford University, for later publication of this investigation.

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